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CLASSIFICATION OF *OUDEMANSIELLA* (BASIDIOMYCOTA: TRICHOLOMATACEAE), WITH SPECIAL REFERENCE TO SPORE STRUCTURE

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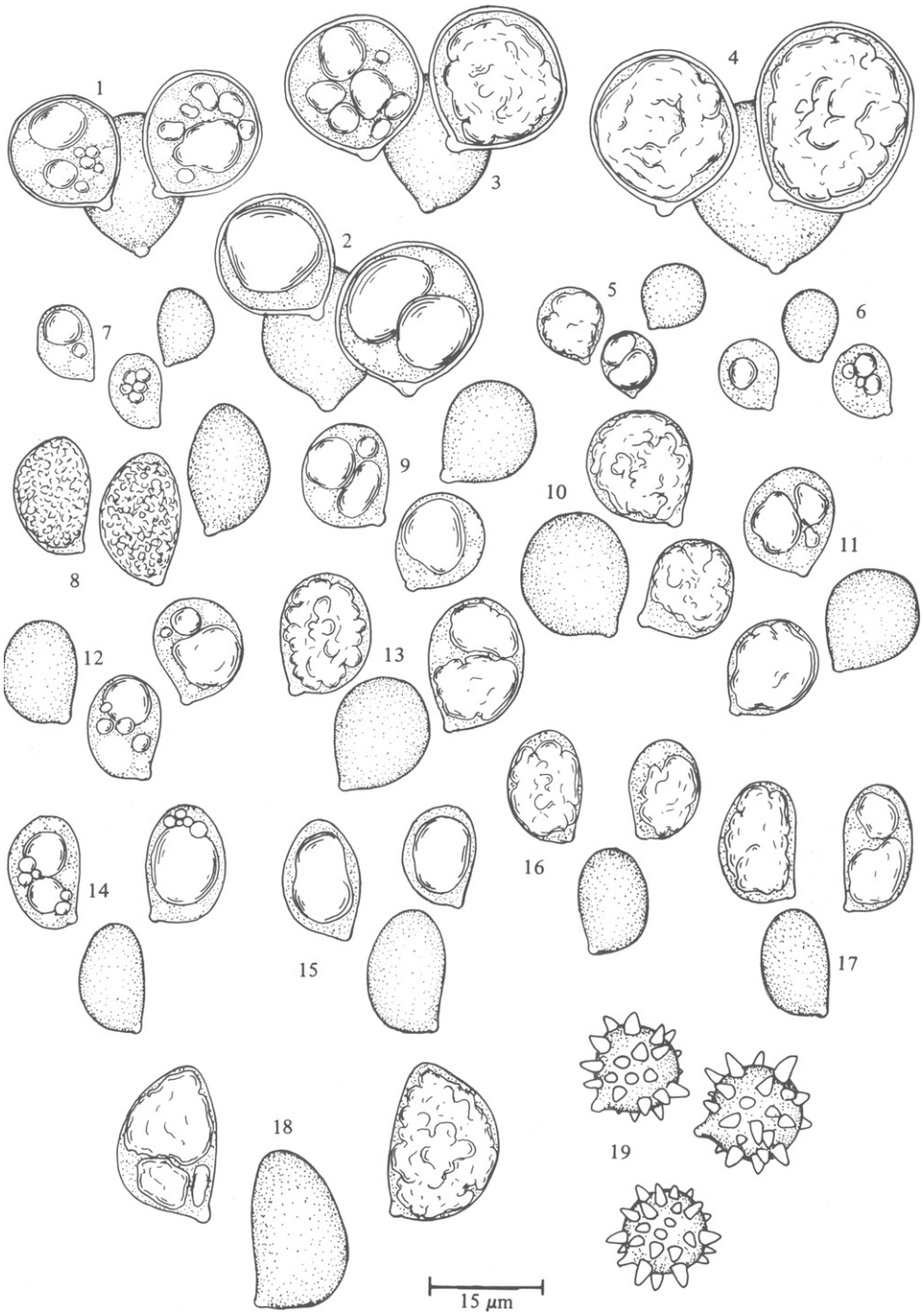
A revised classification of *Oudemansiella* is presented, incorporating both *Oudemansiella* s.str. and *Xerula* within a single genus. The following taxa are proposed: *Oudemansiella* sect. Dactylosporina (Clémençon) stat.nov., *Oudemansiella americana* (Dörfelt) comb.nov., *O. japonica* (Dörfelt) comb.nov., and var. *ahmadii* (Dörfelt) comb.nov., var. *colensoi* (Dörfelt) comb.nov., *O. pudens* (Pers.) comb.nov. and var. *fusca* (Lucand ex Quél.) comb. nov., *O. radicata* var. *africana* (Dörfelt) comb.nov., var. *alba* (Dörfelt) comb.nov., var. *australis* (Dörfelt) comb. nov., var. *furfuracea* (Peck) comb. nov., var. *hygrophoroides* (Singer & Clémençon) comb. nov., var. *rubescens* (Melik-Chacatrajan) comb.nov., var. *superbiens* (Berk.) comb. nov., *O. raphanipes* (Berk.) comb.nov. Keys are provided to subgenera, species and varieties. Species of both *Megacollybia* and *Mycenella* are excluded from the genus. A detailed account of basidiospore structure within the genus, which provides evidence in support of the proposed classification, is presented. The tegumental layers of the spore wall comprise a thick coriotunica, incorporating variable development of a corium and an epitunica, and a myxosporium, which is often differentiated into a podostratum, mucostratum and a fragmenting sporothecium. Epitunica ornamentation is confirmed in the section Albotomentosi.

Oudemansiella Speg. is an agaricoid genus of world-wide distribution which, together with *Mycenella* (J. Lange) Singer, *Physocystidium* Singer, *Strobilurus* Singer, and probably *Megacollybia* Kotl. & Pouzar, form the subtribe Oudemansiellinae Singer of the tribe Marasmieae Schroeter in the Tricholomataceae. The genus is characterized by the production of collybioid basidiomes which have an essentially hymeniodermic pileipellis which may become either extensively disrupted through gelatinization or give rise to conspicuous and crowded setoid sclerocystidia. The spores are hyaline, inamyloid, subglobose to short ellipsoid, and often voluminous, producing a white to cream-coloured spore deposit.

Spegazzini (1880) initially proposed *Oudemansia* to accommodate a single species, *Agaricus platensis* Speg. As this name was preoccupied by an earlier homonym, *Oudemansia* Miquel in the Sterculiaceae (Malvales), Spegazzini (1881) found it necessary to change the name to *Oudemansiella*. Singer (1950) examined the type collection of *A. platensis* and also gathered fresh material from the type locality, finding it identical in every way with the familiar pantropical fungus, now called *O. canarii* (Jungh.) v. Hoehnel.

Patouillard (1887) erected *Mucidula* in order to separate *Agaricus mucidus* Schrader: Fr. from both *Collybia* (Fr.) Kummer and *Armillaria* (Fr.) Kummer on the basis of the presence of velar layers and the voluminous spores. Boursier (1924) expanded *Mucidula* to include *Collybia radicata* (Relhan: Fr.) Quél. and *C. longipes* (Bull.) Kummer, emphasizing similarities in the large spores, basidia, cystidia, and in the hymenioderm. Meanwhile, v. Hoehnel (1910) had emended *Oudemansiella* to include species with velar layers, a gelatinized pileipellis, large cystidia and large spores. The pilosity of the basidiome surfaces, coupled with the absence of a gelatinized layer, in *C. longipes* was regarded as sufficiently distinct by Maire (1933) for him to separate this species from *Mucidula* and to propose a new genus, *Xerula*. *Oudemansiella* and *Xerula* were retained as distinct genera by Singer (1936, 1951) in his earlier classification of the Agaricales. Moser (1955) supported the view of Boursier and placed species from both *Mucidula* and *Xerula* under a single genus, namely *Oudemansiella*, and this solution was subsequently adopted by Singer (1962).

Recently, revised classifications have been provided by Clémençon (1979) and Dörfelt (1979;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1980*a*, *b*; 1981*a*, *b*; 1982; 1983*a*, *b*, *c*; 1984; 1985). Clémençon introduced a computer-aided study, utilizing comparative coordination of 16 characters, relating to the pileus, stipe, spores, cystidia and habitat. Five subgenera within *Oudemansiella* were recognized, including the subgenus *Megacollybia* (Kotl. & Pouzar) Moser, which was seen to represent the most primitive group on the basis of an absence of any gelatinization of the pileipellis, and lack of both sclerocystidia and velar layers. It was Moser who had already included the monotypic genus, *Megacollybia* Kotl. & Pouzar, in *Oudemansiella*, a view strongly resisted by Singer (1975). *Oudemansiella xeruloides* Bon and *O. pseudoradicata* Moser were included in the subgenus *Megacollybia*, along with *Megacollybia platyphylla* (Pers.: Fr.) Kotl. & Pouzar. *Mycenella kuehneri* was also incorporated into the genus, forming the basis for a separate subgenus, *Pseudomycenella* Clémençon.

Dörfelt, in a series of papers, has maintained *Xerula* as a genus separate from *Oudemansiella* but making the important observation, albeit at generic level, that any distinction between the two taxa lay not between the dry, pilose species, *C. longipes*, and the gelatinized, glabrous species, *C. radicata*, as proposed by Maire (1933) and subsequently widely accepted, but rather between *C. longipes* and the group containing *O. mucida* (Schrader: Fr.) v. Hoehnel. Thus Dörfelt's emendation of the genus *Xerula* contained both *C. longipes* and *C. radicata*, and was characterized by basidiomes with hymeniodermic development, with or without sclerocystidia, the formation of a pseudorhiza, and gymnocarpic development. *Oudemansiella* was restricted to the truly lignicolous species, lacking a pseudorhiza, and exhibiting bi-velangiocarpic development. In this way, the character of gelatinization of the pileal surface was regarded as an adaptive feature common to both genera.

The present authors accept Dörfelt's revised distinction between *Xerula* and *Oudemansiella* but only at the level of subgenus. Similiarities in pileipellis structure, the voluminous spores, prominent hymenial cystidia, and geographical distribution would indicate a very close association and a common origin. The unique and somewhat complex tegumental structure of the spore wall shown in all the species examined lends further support for a relationship within a single genus. The development of gelatinization, sclerified dermatocystidia, and velar layers should be seen as adaptive features in response to habitat and climatic requirements. The genus *Dactylosporina* (Clémençon) Dörfelt, based on South American species with spinose spores, should also be retained within *Oudemansiella*, as all the other characters are extremely similar to those found in the *O. radicata* group. Comparable variation in spore form exists in *Mycenella*, another genus in the Oudemansiellinae. The subgenus *Pseudomycenella* has much more in common with *Mycenella* than with *Oudemansiella* and is therefore excluded from the genus. The genus *Megacollybia* is also excluded for reasons of spore, cystidial, hyphal and pileipellis structure. A new classification is proposed recognizing two subgenera and five sections.

BASIDIOSPORE STRUCTURE IN *OUDEMANSIELLA*

Spores of *Oudemansiella* are hyaline to pale stramineous under the light microscope and inamyloid, non-dextrinoid, acyanophilic, the spore deposit ranging from pure white to pale cream in colour. Many species are characterized by their large spore size, ranging from 9–12 μm diam in the section Xerula to very large, up to 26 μm diam in the section Oudemansiella. Spore form varies from subglobose to almost globose in the sections Dactylosporina, Oudemansiella and Xerula, together with certain taxa in the section Radicatae, to ovoid, ellipsoid or amygdaliform in sections Albotomentosi and Radicatae, to ovoid, ellipsoid or amygdaliform in sections Albotomentosi and Radicatae. In the section Dactylosporina, the

Figs 1–19. *Oudemansiella* basidiospores. Figs 1–4. Section Oudemansiella. Fig. 1. *O. mucida* (Netherlands, Maas Geesteranus). Fig. 2. *O. venesolamellata* (Japan, Pegler 3489) Fig. 3. *O. canarii* (*Agaricus apalosarcus*, Sri Lanka, Thwaites 699, holotype). Fig. 4. *O. australis* (New Zealand, Taylor 51, holotype). Figs 5–6. Section Xerula. Fig. 5. *O. pudens* (Sweden, Pettersen). Fig. 6. *O. melanotricha* (Czechoslovakia, Herb. Dörfelt, topotype). Figs 7–8. Section Albotomentosi. Fig. 7. *O. nigra* (East Germany, Dörfelt, paratype). Fig. 8. *O. xeruloides* (France, Bon, holotype). Figs 9–18. Section Radicatae. Fig. 9. *O. japonica* var. *japonica* (Japan, Hongo 752, holotype). Fig. 10. *O. japonica* var. *ahmadii* (Pakistan, Ahmad 4919, holotype). Fig. 11. *O. japonica* var. *colensoi* (New Zealand, Colenso 350, holotype). Fig. 12. *O. endochorda* (Sri Lanka, Thwaites 703, holotype). Fig. 13. *O. raphanipes* (India, Hooker fil. 95, holotype). Fig. 14. *O. radicata* var. *radicata* (England, Kew, Pegler s.n.). Fig. 15. *O. radicata* var. *furfuracea* (U.S.A. Massachusetts, Pegler 3682). Fig. 16. *O. radicata* var. *australis* (Australia, Sinnott 2147, holotype). Fig. 17. *O. radicata* var. *superbiens* (Drummond 119, holotype). Fig. 18. *O. radicata* var. *africana* (Tanzania, Ryvarden 10178, holotype). Fig. 19. Section Dactylosporina, *O. steffenii* (Bolivia, Singer B1612).

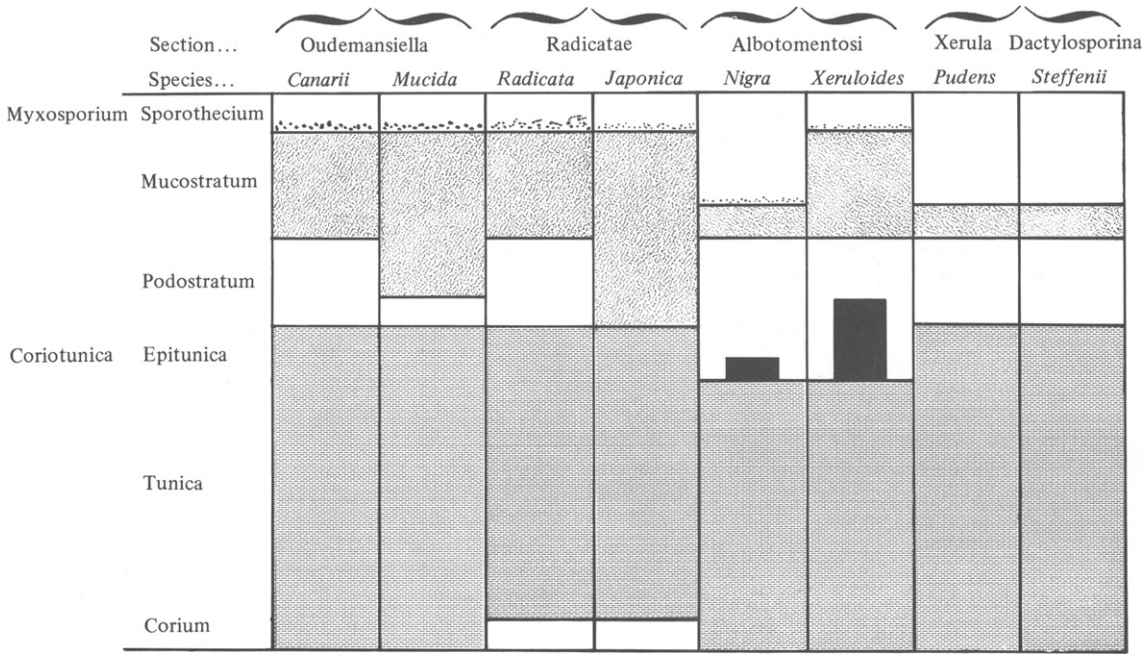


Table 1. *Wall teguments in* Oudemansiella.

smooth wall surface is interrupted by numerous spinose, conical outgrowths, up to 5·5 μm long. The hilar appendix is often prominent and has a subterminal, nodulose hilum. The supra-appendicular region is never noticeably depressed, appearing only applanate in the more elongated spores, and a plage area is not differentiated. The spore surface is smooth, the wall may be thin or thickened (–1·5 μm), and there is no germ pore.

Ultrastructurally, although the tegumental layering of the spore wall is complex, it is based on a pattern which is common to all sections within the genus (see Table 1). As in most basidiospores, the tegumental layering is formed by a combination of the spore wall proper (or eusporium), which in this case is formed by the coriotunica, and the overlying myxosporium, which consists of two or three layers. The tunica (or episporium) is the thickest of the teguments, and is particularly well formed in the section Oudemansiella, so that the spores of that section are often described as 'thick-walled'. The tunica typically appears electron-grey in ultrathin sections and fibrillar in texture, with the fibrils running parallel to the spore surface. Kuehner (1980) observed that in the spores of *O. radicata* the innermost layer, the corium (or endosporium), is differentiated, appearing thin, electron-lucent and structureless. This layer is not visible in the other sections but does seem to be characteristic of the section Radicatae. In the section Albotomentosi, the outermost layer of the tunica becomes differentiated, forming an interrupted and often discontinuous layer, the epitunica (or exosporium), which appears black–opaque and forms a very low, verruculose ornamentation. This epitunica ornamentation, formed from the spore wall proper, is a true ornamentation not observed in the other sections. The innermost layer of the myxosporium is always differentiated in the genus *Oudemansiella*, with a 'white', electron-lucent, and apparently structureless podostratum. This subtends an outer layer, the mucostratum, which appears electron-grey and finely granular in ultrathin sections, and stains orthochromatically with Cotton blue in lactic acid and ruthenium red, suggesting the presence of mucilage. The mucostratum forms a thick layer in the sections Oudemansiella and Radicatae, but much thinner in the sections Albotomentosi, Dactylosporina and Xerula.

Finally, the surface of spores found in sections Albotomentosi, and particularly Oudemansiella and Radicatae is characterized by a granular or crystalline encrustation in SEM and carbon replica preparations. This is not a true wall ornamentation as it is due to the close association of the fine, disintegrating sporothecium (or ectosporium) and the mucostratum, which are both derived from the myxosporium.

A REVISED CLASSIFICATION OF THE GENUS *OUDEMANSIELLA*

Key to Sections

1. Lignicolous, growing directly on stumps and branches; pileipellis gelatinized; sclerocystidia absent; bi-velangiocarpic developments; spores voluminous, subglobose; world-wide . . Subgenus 1 *Oudemansiella* Section 1 Oudemansiella
1. Pseudorhiza present, growing from buried roots; gymnocarpic development . . . Subgenus 2 *Xerula*
   2. Dermatocystidia present in pileipellis; pileipellis not gelatinized; spores smooth, lacking digitate outgrowths:
      3. Sclerified dermatocystidia present in abundance, hyaline to blackish brown forming a trichodermium on the pileal and stipe surfaces; spores small, up to 10μm long. subglobose to short ellipsoid; north temperate . . . . . Section 2 Xerula
      3. Thin-walled dermatocystidia present in pileipellis, often scattered, readily collapsing to form an indefinite tomentum; spores small to large, subglobose to broadly amygdaliform; Europe . . . . . Section 3 Albotomentosi
   2. Dermatocysidia absentl pileipellis gelatinized or not:
      4. Spores, smooth, voluminous, subglobose, ellipsoid or amygdaliform, lacking digitate outgrowths; world wide . . . . . Section 4 Radicatae
      4. Spores stellate, subglobose with numerous digitate outgrowth; South America . . . . . Section 5 Dactylosporina

Subgenus 1. OUDEMANSIELLA

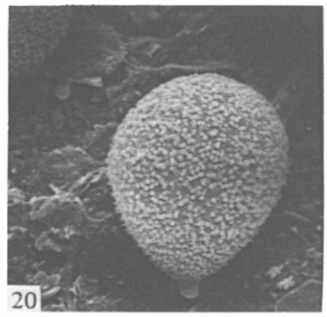
Mudicula Pat., *Hymen. Eur.*: 95 (1887).
Phaeolimacium P. Henn. in Warburg, *Monsunia* **1**: 14 (1899).

Saprobic, growing directly on wood, not developing a pseudorhiza. Development bi-velangiocarpic, with basidiome retaining velar squamules and often a stipe annulus. Gelatinization of both the pileal and stipe surfaces. Pileipellis hymeniodermic but disrupted by gelatinization, with erect elements, occasionally inflated becoming elongate and hyphoid. Sclerified dermatocystidia absent. Spores voluminous, subglobose, thick-walled, lacking digitate outgrowths. Lamellae adnexed to adnate, at times with a decurrent tooth. World-wide, extremely common throughout the pantropical zone and extending, with the Fagales, into temperate zones. The most primitive section.

Type species basionym: *Agaricus platensis* Speg.

Key to Species of Sect. Oudemansiella

1. Stipe with a persistent, membranous annulus; pileus white to pale greyish brown, opalescent; growing on *Fagus*:
   2. Lamellae broad, not interveined; context of pileus relatively firm; stipe white; spores 14–21 × 12–18·7 μm; Europe . . . . . *O. mucida*
   2. Lamellae ridged and anastomosing towards the stipe; context of pileus very thin, soft and putrescent; stipe white above, brown below; spores 15–22 × 14–21 μm; Japan . . . . . *O. venesolamellata*
1. Annulus absent on stipe or occasionally restricted to a fugacious zone:
   3. Pileus initially dark sepia brown soon paling to whitish or cream colour; often retaining membranous velar squamules, especially at the margin; lamellae not interveined; spores 15–24 × 10–22 μm; pantropical *O. canarii*
   3. Pileus white discolouring brownish at centre, lacking velar squamules; lamellae rugulose and interveined; spores 20–26·5 × 19–26 μm; New Zealand . . . . . *O. australis*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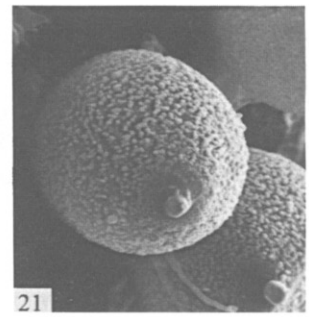
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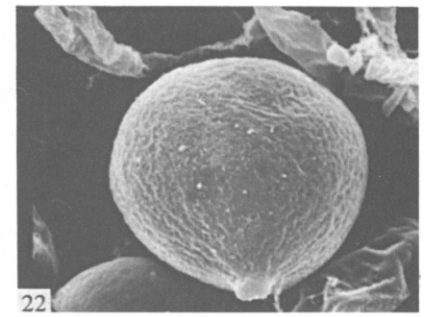
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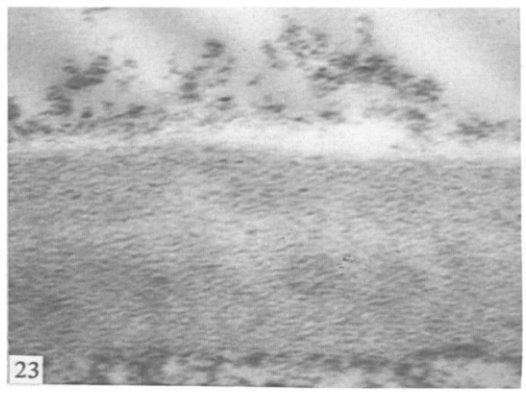
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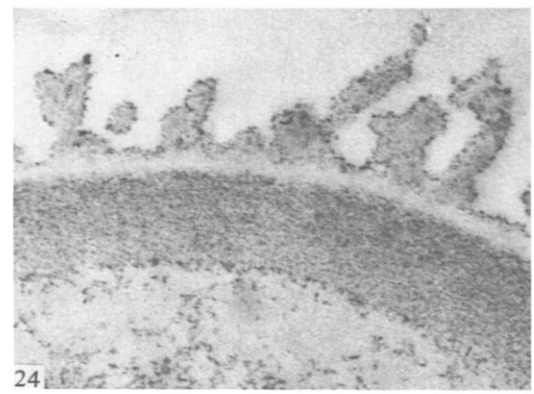
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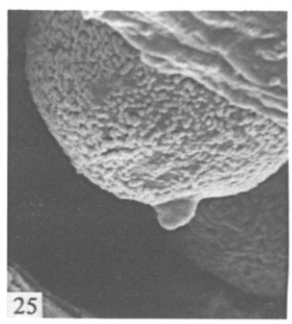
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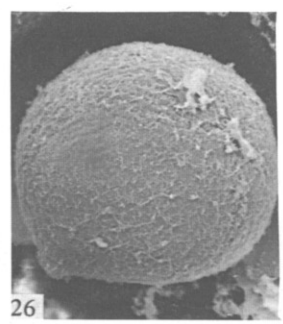
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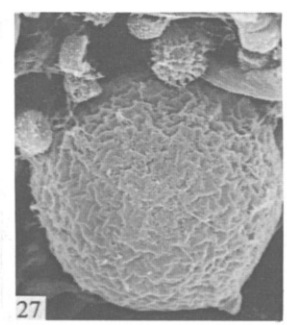
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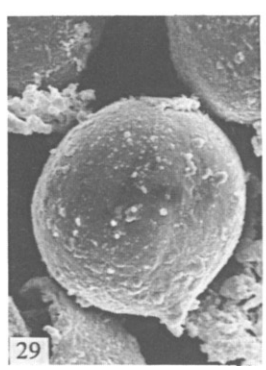
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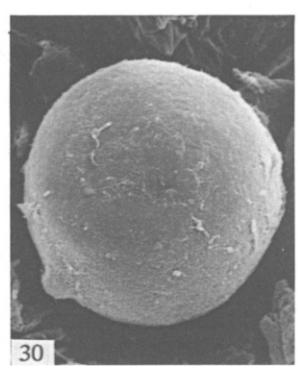
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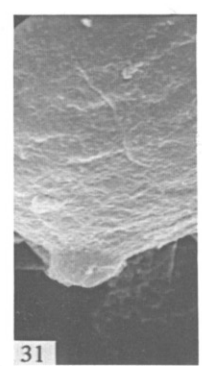
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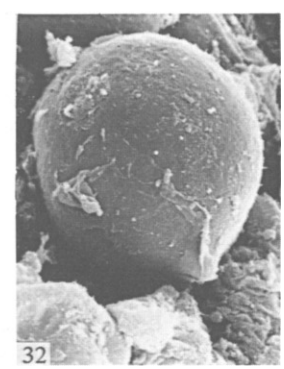
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Section 1 OUDEMANSIELLA

O. MUCIDA (Schrader: Fr.) v. Hoehnel, *Akad. Wiss. Wien Math.-naturw. Kl.* **119**: 885 (1910).

Agaricus mucidus Schrader: Fr., *Syst. Mycol.* **1**: 28 (1821); Schrader, *Spic. Fl. Germ.*: 116 (1794). (Figs 1, 20–23)

Spores 14–21 × 12–18·7 (17 ± 1·2 × 16·6 ± 1·0) μm, $Q = 1·10$, subglobose to almost globose, lacking a suprahilar depression, at most adaxially applanate; hilar appendix prominent; contents with conspicuous, highly refractive oil-guttules. Podostratum thinner than that found in *O. canarii* but otherwise similar.

Specimens examined: England: Bagham Abbey Woods, 28 Oct. 1936, Pearson; Surrey, Box Hill, 20 Sept. 1961, Pegler; Hertfordshire, Whippendell Wood, 8 July 1968, Young. Netherlands: Zuid-Holland, 13 Oct. 1951, Maas Geesteranus. Sweden: Göteborg, 24 Sept. 1942, Karvall & Nathorst-Windahl.

O. VENESOLAMELLATA (Imaz. & Toki) Imaz. & Hongo, *Journ. Japan Bot.* **32**: 146 (1957). (Figs 2, 30)

Mucidula venesolamellata Imaz. & Toki, *Bull. Gov. Exp. St., Meguro* **79**: 1 (1955).

Spores 15–22 × 14–21 (18 ± 1·2 × 16·5 ± 1·0) μm, $Q = 1·09$; globose or nearly so, with a slight adaxial applanation; wall up to 1·0 μm thick; usually containing 1–3 large refractive oil-guttules.

Specimen examined: Japan, Yameneshi Pref., Mt Fuji, Shojin-gu-chi, on *Fagus crenata*, 5 Sept. 1983, Pegler 3489 (type locality).

O. CANARII (Jungh.) v. Hoehnel, *Akad. Wiss. Wien Math.-naturw. Kl.* **118**: 276 (1909). (Figs 3, 24–29)

Agaricus canarii Jung., *Batav. Geroot. Kunst. Wetens. Verh.* **17**: 82 (1838).

A. apalosarcus Berk. & Br., *Journ. Linn. Soc., Bot.* **11**: 520 (1871).

A. platensis Speg., *An. Sci. Cient. Argent.* **9**: 161 (1880).

Oudemansia platensis (Speg.) Speg., loc. cit.: 280.

Phaeolimacium bulbosum P. Henn. in Warburg, *Monsunia* **1**: 14 (1899).

For a full synonymy see Pegler (1983).

Spores (12–) 15–24 × 10–22 (18 ± 1·2 × 16 ± 1·2) μm, $Q = 1·12$, globose or nearly so, lacking a suprahilar depression; hilar appendix prominent; with refractive oily contents. The very thick coriotunica shows no differentiation of any electron-lucent, inner corium; both the mucostratum and crystalline sporothecium are well developed.

Specimens examined: Sri Lanka: Peradeniya, 1868, Thwaites 699, K, type of *A. apalosarcus*. Singapore: Bukit Timah Nat. Res., 15 Mar. 1984, Sidek Bin Kiah 682. Uganda: Budongo For., 15 June 1968, Pegler 1500. Zambia: Kitwe, 5 Jan. 1978, Pearce 574. U.S.A.: Florida, Dale Co., 30 Oct. 1942, Singer F1356. Cuba: Wright 11, K, type of *A. cheimonophyllus*. Costa Rica: Heredia, 25 July 1969, Gomez 3129. Brazil: Rio Grande do Sul, São Leopoldo, 1905, Rick; 1930, Rick. Trinidad: Simba Res. Stn, 1 June 1984, Baroni 446; 27 Oct. 1949, Dennis 240.

O. AUSTRALIS Stev. & G. Taylor, *Kew Bull.* **19**: 33 (1964). (Figs 4, 31)

Spores 20–26·5 × 19–26·5 × 19–26 (25 ± 1·5 × 22·5 ± 1·0) μm, $Q = 1·10$, subglobose to almost globose, with a prominent hilar appendix; with a thickened wall (~1 μm); filled with very refractive contents.

Specimen examined: New Zealand, Wellington, Wainui Valley, 25 Mar. 1961, Taylor 51, K, holotype.

Subgenus 2. XERULA (R. Maire) Singer, *Sydowia* **15**: 59 (1962).

Xerula R. Maire, *Treb. Mus. Cienc. Nat. Barcel.* ser. Bot. **15**: 66 (1933).

Xerula subgenus *Xerula* Dörfelt, *Feddes Repert.* **90**: 367 (1979).

Saprobic, growing from dead tree roots by a tapering subterranean pseudorhiza. Development gymnocarpic, lacking both velar squamules and a stipe annulus. Pileal and stipe surfaces gelatinized or dry. Pileipellis hymeniodermic, with inflated elements. Sclerified dermatocystidia present or absent. Spores variable, ranging from voluminous, ovoid to amygdaliform, to medium (less than 10 μm long) and subglobose, smooth or rarely with digitate outgrowths. Lamellae adnexed to adnate.

Section 2. XERULA Clémençon, *Sydowia* **32**: 77 (1979).

Xerula section Hyalosetae Dörfelt, *Feddes Repert.* **95**: 198 (1984).

Figs 20–32. *Oudemansiella. Section* Oudemansiella, basidiospores.
Fig. 20. *O. mucida*, Hertfordshire, Young, × 4800. Fig. 21. *O. mucida*, Hertfordshire, Young × 4800. Fig. 22. *O. mucida*, Netherlands, Maas Geesteranus, × 6000. Fig. 23. *O. mucida*, Bagham Abbey Woods, Pearson, wall section, × 75000. Fig. 24. *O. canarii*, Dennis 240, × 39200. Fig. 25. *O. canarii*, Gomez 3129, × 2400. Fig. 26. *O. canarii*, Rick, × 4000. Fig. 27. *Agaricus cheimonophyllus*, type, × 4400. Fig. 28. *O. canarii*, Gomez, 3129, carbon replica, × 49000. Fig. 29. *Agaricus apalosarcus*, type, × 3600. Fig. 30. *O. venesolamellata*, Pegler 3489, × 4400. Fig. 31. *O. venesolamellata*, spore base, Pegler 3489, × 10000. Fig. 32. *O. australis*, Taylor 51, × 3000.

Pseudorhiza present, well developed. Spores relatively small, less than 12 μm long, subglobose to short ellipsoid, lacking digitate outgrowths. Sclerified dermatocystidia present, crowded, ranging from hyaline, yellow, brown to black, forming a trichodermium on the pileal and stipe surfaces. Pileipellis hymeniodermic, not gelatinized; north temperate.

Type species basionym: *Agaricus longipes* Bull. (1785) non Scop. (1772).

Key to Species of Sect. Xerula

1. Sclerocystidia pigmented; Europe
   2. Pileus and stipe greyish brown to dull cinnamon brown, velutinate, with concolorous sclerocystidia, 250–300 μm long; spores 8–10 × 7–10 μm, subglobose . . . . . *O. pudens*
      3. Sclerocystidia greyish brown to golden brown . . . . . *O. pudens* var. *pudens*
      3. Sclerocystidia chocolate brown . . . . . *O. pudens* var. *fusca*
   2. Pileus and stipe tawny brown, hispid, with fuscous to black sclerocystidia, 1–3 mm long; spores 9–11 × 7·5–9·5 μm, subglobose to ovoid . . . . . *O. melanotricha*
1. Sclerocystidia hyaline or very pale yellowish, 50–200 μm long; pileus and stipe grey fuliginous, velutinate with a silvery sheen; spores 9–12·5 × 7–8·5 μm, ellipsoid; north-eastern USA . . . . . *O. americana*

Oudemansiella pudens (Pers.) comb.nov. (Figs 5, 32–37)

Agaricus pudens Pers., *Syn. Meth. Fung.* **2**: 313 (1801).

A. longipes Bull., *Herb. Fr., Champ.*; pl. 232 (1785), non *A. longipes* Scop., *Fl. Carniol.* edit. 2, **2**: 446 (1772).

A. radicatus Relhan ssp. *pudens* Pers., *Syn. Meth. Fung.* **2**: 313 (1801).

Mucidula longipes (Bull.) R. Maire, *Publ. Junta Cienc. Nat. Barcel., Treb. Mus. Cienc. Nat. Barcel.* **15**: 66 (1933).

X. pudens (Pers.) Singer, *Lilloa* **22**: 289 (1951).

O. badia sensu Moser, *Zeitschr. Pilzk.* **19**: 11 (1955), non Quél. (1880).

O. longipes (Bull.) Moser in Gams, *Kl. Kryptogamenfl.* **11b**/2, rev. ed. 5: 156 (1983).

For a detailed synonymy see Dörfelt (1982).

Spores 8–11·5 × 7–11 (9·5 ± 0·8 × 8·5 ± 0·6) μm, $Q = 1·10$, globose or nearly so, usually with an adaxial applanation. Ultrastructurally, this species shows the simplest wall construction, comprising a very thick coriotunica, a differentiated podostratum, and a thin mucostratum but no differentiation of a corium, epitunica or sporothecium.

Specimens examined: England: Kent, Otford, 20 Sept. 1981, A. Heinrici; Kent, Shoreham, 25 July 1965, Sinnott & Thoday 604; Huntingdonshire, Monks Wood, 7 Sept. 1974, Pegler; Bedfordshire, Heath & Reach, 7 Oct. 1973, Reid. Sweden: Gotland, Atlingbo, 1950, Pettersen. Italy: Abruzzi, 27 Oct. 1981, Dennis & Pacioni.

O. pudens var. **fusca** (Lucand ex Quél.) comb.nov.

Marasmius longipes (Bull.) Quél., *Fl. Mycol. Fr.*: 321 (1888).

X. longipes (Bull.) R. Maire var. *fusca* (Lucand ex Quél.) Dörfelt, *Feddes Repert.* **91**: 213 (1980).

X. pudens var. *fusca* (Lucand ex Quél.) Dörfelt, *Mycotaxon* **15**: 63 (1982).

O. MELANOTRICHA (Dörfelt) Moser in Gams, *Kl. Kryptogamenfl.* **11b**/2, rev. ed. 5: 156 (1983). (Figs 6, 38, 39)

X. melanotricha Dörfelt, *Feddes Repert.* **90**: 367 (1979).

?*Collybia longipes* (Bull.) Kummer var. *badia* Quél., *Bull. Soc. Amis Sci. Nat., Rouen* sér. 2, **15**: 154 (1880).

Spores 9–11 × 7·5–9·5 (9·5 ± 0·6 × 8·5 ± 0·4) μm, $Q = 1·1$, subglobose to broadly ovoid, adaxially applanate, with a small but distinct hilar appendix; usually containing several small, refractive oil-guttules.

Specimen examined: Czechoslovakia, Velka Fatra, Sept. 1979, ex-herb. Dörfelt, K, topotype.

O. americana (Dörfelt) comb.nov.

X. americana Dörfelt, *Feddes Repert.* **92**: 255 (1981).

O. longipes var. *americana* Mitchel & A. H. Smith, *Mycologia* **70**: 1045 (1978, epithet invalid, ICBN 43·1).

Figs 33–40. *Oudemansiella* section Xerula.
Fig. 33. *O. pudens*, Sinnott & Thoday 604, × 6900. Fig. 34. *O. pudens*, Sinnott & Thoday 604, × 3060. Fig. 35. *O. pudens*, Sinnott & Thoday 604, × 7800. Fig. 36. *O. pudens*, Reid, × 7200. Fig. 37. *O. pudens*, Reid, × 7200. Fig. 38. *O. pudens*, wall section, Reid, × 49000. Fig. 39. *O. melanotricha*, type, developing basidiospores, × 5000. Fig. 40. *O. melanotricha*, Dorfelt, × 3300.


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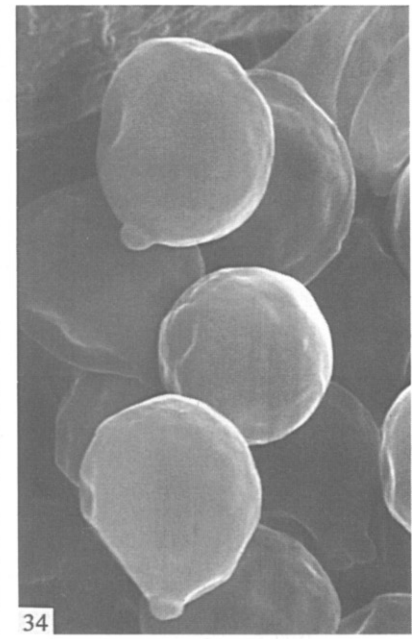
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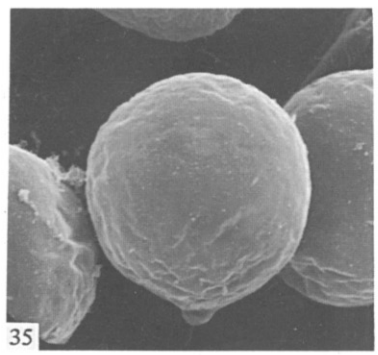
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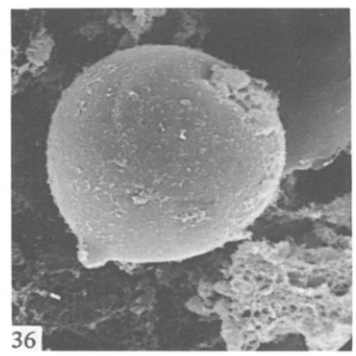
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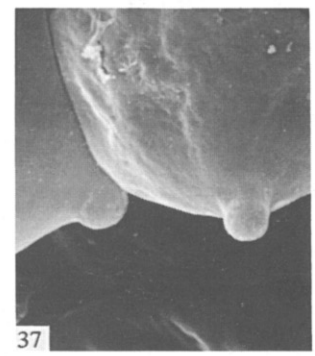
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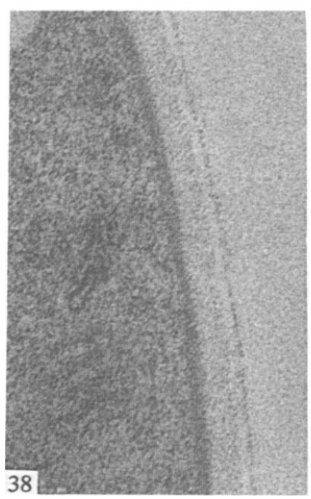
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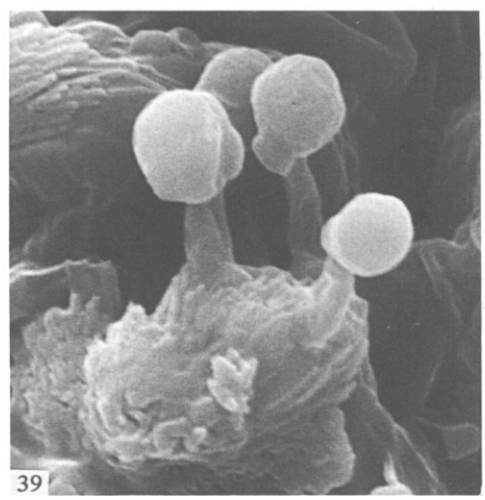
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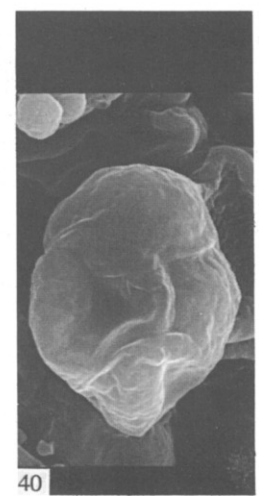
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Section 3. ALBOTOMENTOSI Clémençon, *Sydowia* **32**: 78 (1979).

Oudemansiella section Protoxerula Clémençon, loc. cit.: 77.

Xerula section Albotomentosi (Clémençon) Dörfelt, *Feddes Repert* **91**: 434 (1980).

Xerula section Protoxerula (Clémençon) Dörfelt, loc.cit.: 435.

Pseudorhiza present, well developed. Spores smooth, lacking digitate outgrowths. Pigmented and sclerified dermatocystidia absent; hyaline, thin-walled or very slightly thick-walled dermatocystidia present but readily collapsing to form an appressed tomentum, never a trichodermium. Pileipellis hymenodermic, with inflated elements, not gelatinized. Europe.

Type species basionym: *O. nigra*.

Key to Species of Sect. Albotomentosi

1. Spores less than 12 μm long, subglobose to ovo-ellipsoid; pileus more than 3 cm diam; associated with *Fagus*:
   2. Pleurocystidia abundant and projecting; cheilocystidia capitate; pileus and stipe grey to yellowish grey; spores 8·5–9·5 × 6–7·5 μm, subglobose to ovoid . . . . . *O. caussei*
   2. Pleurocystidia absent or very rare, not projecting; spores ovo-ellipsoid:
      3. Pileus dark, cigar brown to fuliginous, rugulose, indistinctly pubescent; cheilocystidia utriform; spores 8·5–12 × 7–8·5 μm . . . . . *O. nigra*
      3. Pileus greyish cream at centre, fuscous grey towards the margin, uniformly pubescent; cheilocystidia fusoid to utriform; spores 9–10 × 6·5–7·5 μm . . . . . *O. renati*
1. Spores large, 14–19 × 9·5–12·5 μm, broadly amygdaliform; pileus 1–3 cm diam, ochraceous brown; cheilocystidia utriform; pleurocystidia none; in sand dunes . . . . . *O. xeruloides*

O. CAUSSEI (R. Maire) Moser apud Clémençon, *Nova Hedwig.* **28**: 19 (1977); Moser, *Zeitschr. Pilzk.* **19**: 11 (1955, nom. non. val. publ., ICBN Art. 34.1).

Xerula caussei R. Maire, *Bull. Soc. Mycol. Fr.* **53**: 265 (1937).

O. NIGRA Dörfelt, *Ceská Mykol.* **27**: 28 (1973). (Figs 7, 40–43)

X. nigra (Dörfelt) Dorfelt, *Landsch. Natur. Thuringen* **14**: 60 (1977).

O. stridula sensu Moser, *Zeitschr. Pilzk.* **19**: 11 (1955), non *Agaricus stridulus* Fr., *Epicrisis*: 85 (1838).

Spores 8·5–12 × 7–8·5 (10·5 ± 0·8 × 7·5 ± 0·5) μm, $Q = 1·4$, broadly ovoid to short ellipsoid, with an adaxial applanation, thin-walled, containing numerous refractive oil-guttules. Ultrastructurally, the tegumental layering of the spore wall is of interest in its similarity to that observed in *O. xeruloides*. The outermost layer of the coriotunica is differentiated into a very narrow, electron-opaque epitunica, which shows some discontinuity, indicating a very slight eusporial ornamentation. This ornamentation is too low to be visible under a light microscope, especially as it is overlain by the podostratum, mucostratum and sporothecium.

Specimen examined: German Democratic Republic: Jena, 1 Sept. 1972, Dörfelt, K, paratype.

O. RENATI Clémençon, *Nova Hedwigia* **28**: 14 (1977).

X. nigra var. *renati* (Clémençon) Dorfelt, *Feddes Repert.* **91**: 429 (1980).

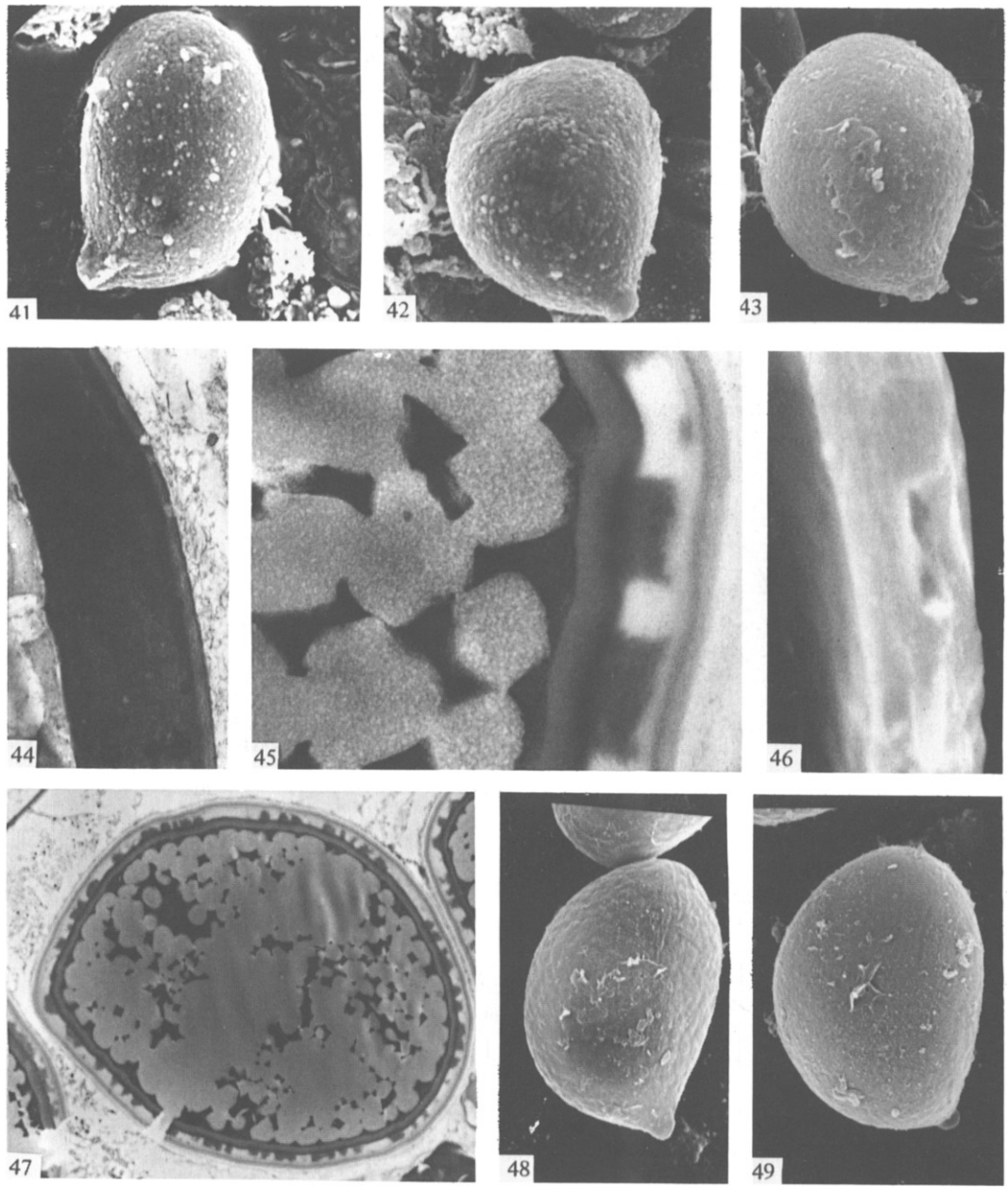
O. XERULOIDES Bon, *Documen. Mycol.* **4** (fasc. 17): 13 (1975). (Figs 8, 44–48)

X. xeruloides (Bon) Dörfelt, *Feddes Repert.* **91**: 216 (1980).

Spores 14–19 × 9·5–12·5 (16·5 ± 1·5 × 11 ± 1·0) μm, $Q = 1·5$, ovo-ellipsoid to broadly amygdaliform, often with a subacute apex but also with an obtusely rounded apex; wall slightly thick-walled and the surface appearing minutely verruculose under the light microscope; contents highly refractive. Ultrastructurally, the spores show a strong development of a disrupted epitunica, appearing as electron-opaque verruculae growing into an overlying myxosporium. Such verruculae are only known in this species of *Oudemansiella*, although slight epitunica differentiation is present in the spores of the closely related *O. nigra*.

Oudemansiella xeruloides was proposed as the type and only species of the section Protoxerula Clémençon by Clémençon (1979), on the basis of the presence of septate dermatocystidia. Reid (1985) redescribed the dermatocystidia found in this species, showing them not to be septate, and proposed the transfer of *O. xeruloides* to the section Albotomentosi, there being no other distinguishing character, The epitunica development in the spore wall provides additional evidence for this transfer.

Specimens examined: France: Olone, Nov. 1973, Bon, holotype, Jersey: St Helier, 9 Oct. 1977, d'A. Laffoley.



Figs 41–49. *Oudemansiella* section Albotomentosi.
Fig. 41. *O. nigra*, holotype, × 8600. Fig. 42. *O. nigra*, × 8600. Fig. 43. *O. nigra*, paratype, × 8600. Fig. 44. *O. nigra*, holotype, wall section, × 18000. Fig. 45. *O. xeruloides*, Bon, wall section, × 36000. Fig. 46. *O. xeruloides*, d'A. Laffoley, SEM, wall section, × 30000. Fig. 47. *O. xeruloides*, d'A. Laffoley, section, × 59000. Fig. 48. *O. xeruloides*, d'A. Laffoley, × 5400. Fig. 49. *O. xeruloides*, d'A. Laffoley, × 5400.

Section 4. RADICATAE Clémençon, *Sydowia* **32**: 78 (1978).

Oudemansiella section Pseudoradicatae Clémençon, loc. cit.: 77.

Oudemansiella section Hygrophoroides Clémençon, loc. cit.: 78.

Xerula section Radicatae (Clémençon) Dorfelt, *Feddes Repert.* **91**: 433 (1980).

Pseudorhiza present. Spores voluminous, ovoid, ellipsoid or amygdaliform. Pileipellis hymeniodermic, gelatinized or not, with inflated elements. Conspicuous dermatocystidia absent. Widespread.

Type species basionym: *Agaricus radicatus* Relhan: Fr.

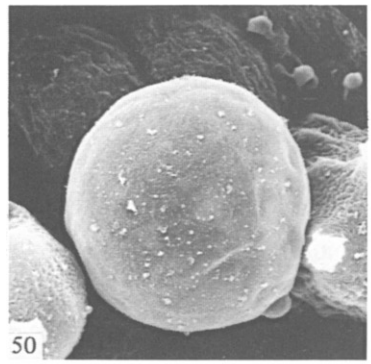
Dörfelt (1981*b*) provided the evidence that *O. pseudoradicata* Moser was only a form of *O. radicata*, thus the section Pseudoradicatae Clémençon, separated only on the basis of reduced gelatinization of the pileipellis, became unneces-

Key to Species of Sect. Radicatae

1. Spores subglobose, 13–20 × 12–19 μm; pileus dark brown; stipe dark brown with furfuraceous squamules . . . . . *O. japonica*
   2. Pileus viscid; stipe base not pilose; spores 13·5–15·5 × 12–15 μm; Japan . . . *O. japonica* var. *japonica*
   2. Pileus dry; stipe base pilose:
      3. Spores 14–20 × 12–19 μm; pileus soon applanate; Pakistan . . . . . *O. japonica* var. *ahmadii*
      3. Spores 12·5–16 × 11–14 μm; pileus subumbonate, fleshy; New Zealand . . . *O. japonica* var. *colensoi*
1. Spores ovoid to ellipsoid; pileus viscid:
   4. Pileus dark brown to blackish brown; stipe lilac-grey to brown, with conspicuous transverse zoning; spores short, broadly ovoid, 12–16 × 8·5–11 μm; Sri Lanka . . . . . *O. endochorda*
   4. Pileus more brightly coloured; stipe glabrous or squamose but lacking transverse zoning; spores larger or more elongate:
      5. Stipe covered with minute, reflexed squamules, reddish brown; pileus olive-brown, wrinkled; spores 15–20·5 × 10·5–14·5 μm, ovoid; S.E. Asia . . . . . *O. raphanipes*
      5. Stipe smooth to furfuraceous, but lacking reflexed squamules; pileus greyish brown or reddish brown; spores 13–24 × 9–14 μm, ovoid to ellipsoid; widespread . . . . . *O. radicata*
         6. Hymenioderm of relatively short piriform elements, eventually disrupting with age:
            7. Spores 13–20 × 8–13 μm, ellipsoid with a broadly rounded apex:
               8. Lamella-edge coloured with cheilocystidia containing a vacuolar pigment; Europe . . . . . *O. radicata* var. *marginata*
               8. Lamella-edge not coloured, cheilocystidia hyaline:
                  9. Pileus whitish to brownish-white, subhygrophanous; cheilocystidia utriform, pedicellate; Europe . . . . . *O. radicata* var. *alba*
                  9. Pileus brown, usually yellowish to reddish brown, sometimes darker; cheilocystidia piriform to clavate:
                     10. Lamellae white:
                        11. Stipe glabrous, lacking both squamules and any villosity; Europe . . . . . *O. radicata* var. *radicata*
                        11. Stipe not glabrous:
                           12. Stipe covered with minute, furfuraceous, appressed squamules; North America . . . . . *O. radicata* var, *furfuracea*
                           12. Stipe with a villose base, not furfuraceous; Victoria, Australia . . . . . *O. radicata* var. *australis*
                     10. Lamellae yellowish; spores more elongate, 14·5–20 × 9–11 μm; Western Australia . . . . . *O. radicata* var. *superbiens*
            7. Spores larger, 19–24 × 12–14 μm, amygdaliform, often with a pointed apex; pileus greyish brown; East Africa . . . . . *O. radicata* var. *africana*
         6. Hymenoderm with elongated hyphoid elements; Europe:
            13. Spores 15–18 × 10–11 μm, ellipsoid; pseudorhiza well developed; pileus and stipe reddish brown; lamellae yellow . . . . *O. radicata* var. *rubescens*
            13. Spores 14·5–21 × 8–11 μm, amygdaliform; pseudorhiza reduced; pileus grey brown . . . . . *O. radicata* var. *hygrophoroides*

Figs 50–58. *Oudemansiella* section Radicatae.

Fig. 50. *O. japonica* var. *japonica*, holotype, ×4800. Fig. 51. *O. japonica* var. *ahmadii*, Ahmad 12089, ×6000. Fig. 52. *O. japonica* var. *colensoi*, Colenso 356, ×7800. Fig. 53. *O. japonica* var. *japonica*, wall section, ×36000. Fig. 54. *O. endochorda*, Thwaites 703, ×6000. Fig. 55. *O. raphanipes*, Hooker f. 96, ×4800. Fig. 56. *O. radicata*, Oxfordshire, Young, wall section, ×49000. Fig. 57. *O. radicata*, Kent, Young, spore surface, carbon replica, ×17500. Fig. 58. *O. radicata*, Oxfordshire, Young, carbon replica, ×2625.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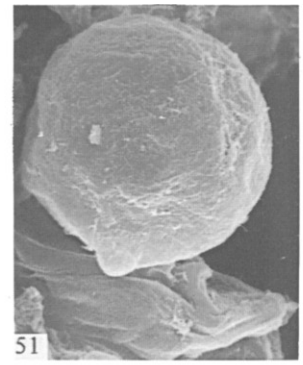
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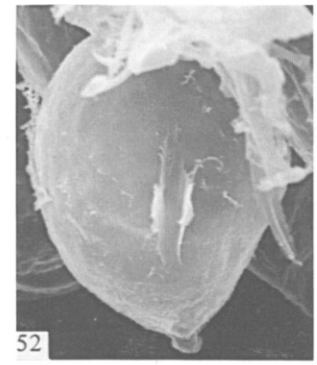
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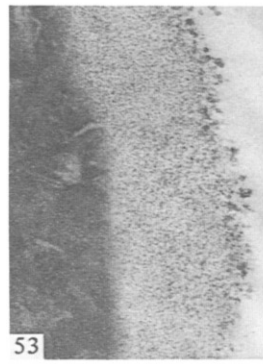
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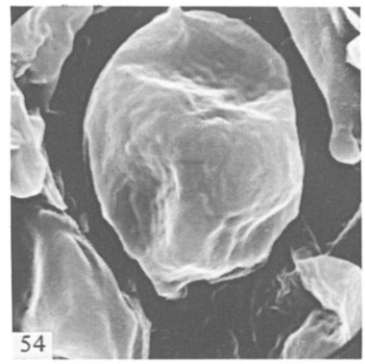
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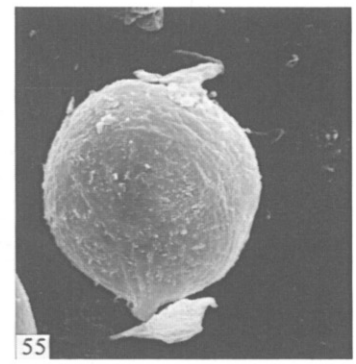
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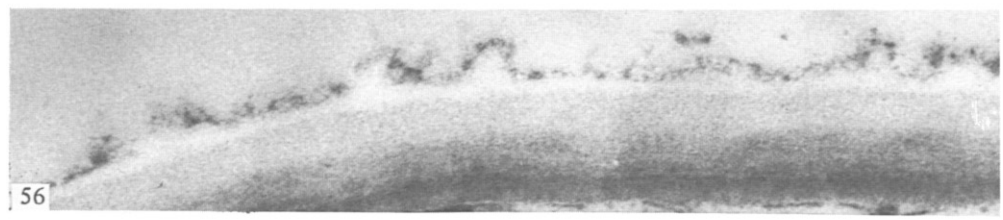
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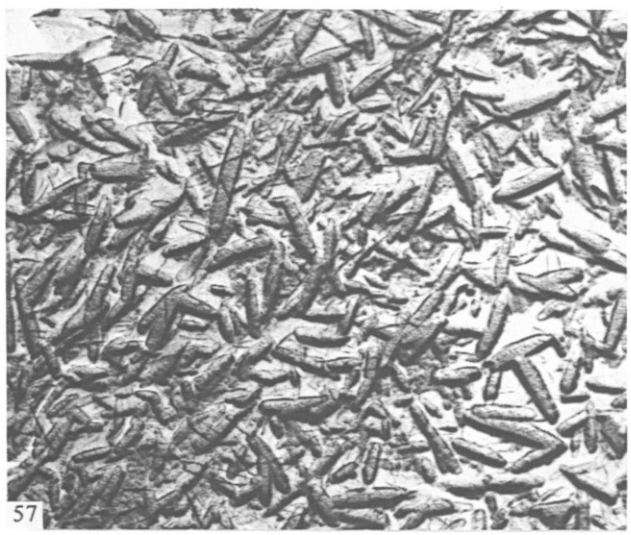
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sary. Similarly, *O. hygrophoroides* Clémençon & Singer, the type species of the section Hygrophoroides Clémençon, was shown to be no more than a variety of *O. radicata*.

Oudemansiella japonica (Dörfelt) comb.nov. (Figs 9, 49, 50, 53)

Xerula japonica Dörfelt, *Feddes Repert.* **95**: 190 (1984).

Spores 13·5–15·5 × 12–15 (15 ± 1·0 × 13·5 ± 0·8) μm, $Q = 1·1$, subglobose to almost globose or short ovoid, with a slight adaxial applanation, thin-walled, containing refractive oil guttules. Ultrastructurally, the spore wall is characterized by the differentiation of a thin, electron-lucent corium forming the innermost layer of the eusporium. The myxosporium consists of a broad mucostratum, without any formation of a podostratum, unlike the spores of the closely related species, *O. radicata*.

Specimen examined: Japan: Otsu, Mt Hiei-san, Hongo 752, K, holotype.

O. japonica var. **ahmadii** (Dörfelt) comb.nov. (Figs 10, 51)

Xerula japonica var. *ahmadii* Dörfelt, *Feddes Repert.* **95**: 192 (1984).

Spores 14–20 × 12–19 (17 ± 0·8 × 15 ± 0·6) μm, $Q = 1·13$, subglobose to short ovoid, thin-walled, with refractive oil-guttules.

Specimens examined: Pakistan, Kalem, Swat, 22 Aug. 1952, Ahmad 4919, K, holotype; Patriata, 15 Aug. 1954, Ahmad 12089, K, paratype.

O. japonica var. **colensoi** (Dörfelt) comb.nov. (Figs 11, 52)

Xerula japonica var. *colensoi* Dörfelt, *Feddes Repert.* **95**: 193 (1984).

Spores 12·5–16 × 11–14 (14 ± 0·7 × 12 ± 0·4) μm, $Q = 1·16$, globose or nearly so, occasionally short ovoid; thin-walled, containing large, refractive oil-guttules.

Specimens examined: New Zealand: 1885, Colenso 350, K, holotype; Colenso 356, K, paratype.

O. ENDOCHORDA (Berk. & Br.) Pegler, *Kew Bull. Addit. Ser.* **12**: 132 (1986). (Figs 12, 54)

Agaricus endochordus Berk. & Br., *Journ. Linn. Soc. Bot.* **11**: 519 (1871).

Collybia endochorda (Berk. & Br.) Sacc., *Syll. Fung.* **5**: 232 (1887).

Amanitopsis endochorda (Berk. & Br.) Petch, *Ann. Roy. Bot. Gard., Peradeniya* **4**: 374 (1910).

Collybia radicata sensu Corner, *Trans. Br. mycol. Soc.* **19**: 64 (1934), non *C. radicata* (Relhan: Fr.) Kummer.

Spores 12–16 × 8·5–11 (14 ± 0·8 × 10 ± 0·6) μm, $Q = 1·4$, ovoid to broadly ellipsoid, thin-walled or with very slightly thickened wall, containing many refractive oil-guttules.

Specimens examined: Sri Lanka: Peradeniya, Aug. 1868, Thwaites 703, K, holotype; Hakgala, Sept. 1914, Petch 4117.

O. raphanipes (Berk.) comb.nov. (Figs 13, 55)

Agaricus raphanipes Berk. in Hooker, *Journ. Bot. & Kew Misc.* **2**: 48 (1850).

Collybia raphanipes (Berk.) Sacc., *Syll. Fung.* **5**: 202 (1887).

Xerula raphanipes (Berk.) Dörfelt, *Feddes Repert.* **94**: 557 (1983).

O. brunneomarginata Vasiljeva, *Notul. Syst. Cryptog. Inst. Bot. Sci. URSS* **6**: 197 (1950).

Spores 15–20·5 × 10·5–14·5 (15·6 ± 1·2 × 13·5 ± 0·8) μm, $Q = 1·22$, broadly ovoid to short ellipsoid, thin-walled, with refractive oil-guttules.

Specimen examined: India: Sikkim, Hooker fil. 96, K, holotype.

O. RADICATA (Relhan: Fr.) Singer, *Ann. Mycol.* **34**: 333 (1936). (Figs 14, 56–62)

Agaricus radicatus Relhan: Fr., *Syst. Mycol.* **1**: 118 (1821); Relhan, *Fl. Cantab.* suppl. **1**: 28 (1786).

Collybia radicata (Relhan: Fr.) Kummer, *Führ. Pilzk.*: 117 (1871).

Gymnopus radicatus (Relhan: Fr.) Murr., *N. Amer. Fl.* **9**: 366 (1916).

Mucidula radicata (Relhan: Fr.) Boursier, *Bull. Soc. Mycol. Fr.* **40**: 333 (1924).

O. pseudoradicata Moser, *Zeitschr. Pilzk.* **19**: 5 (1955).

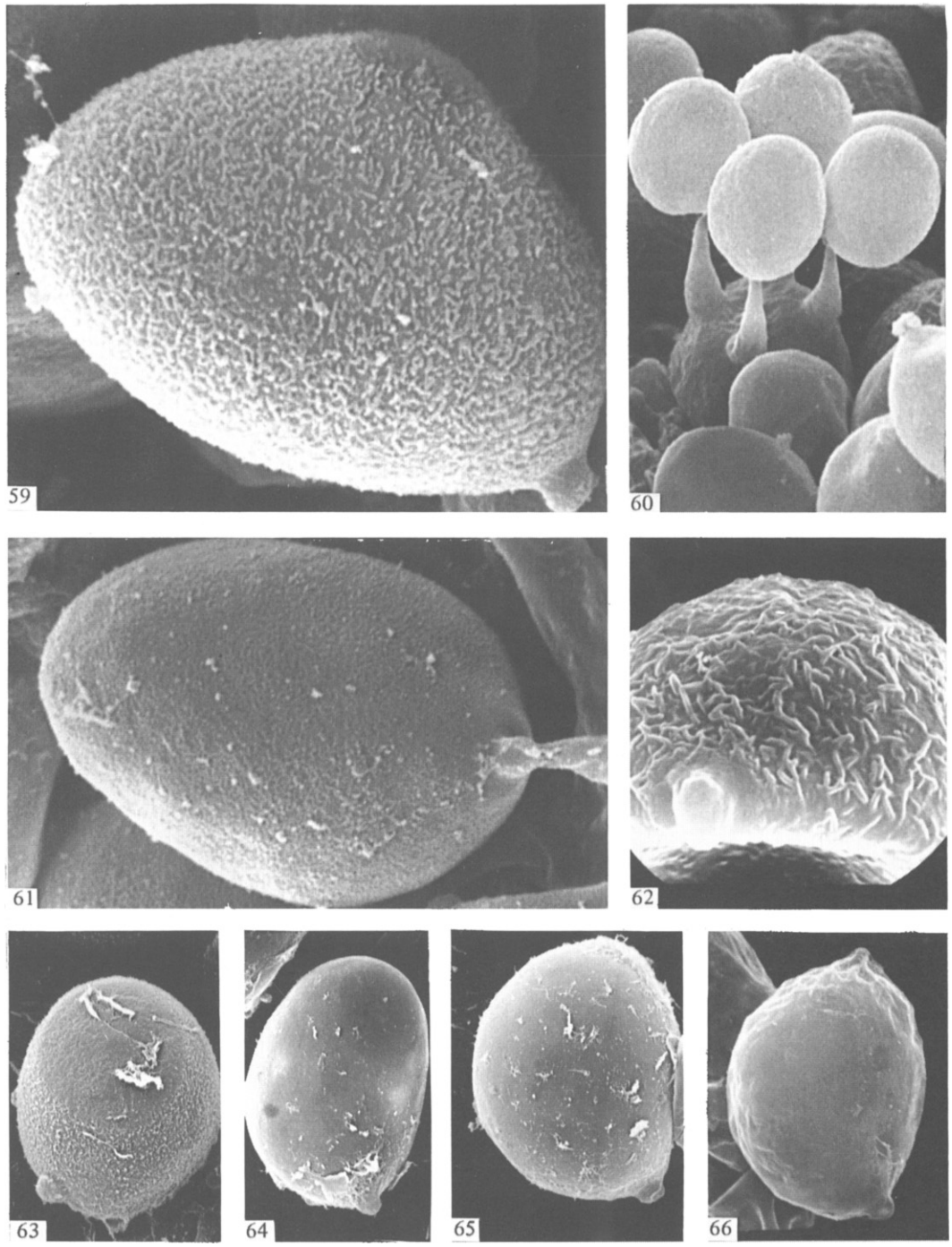
For a full synonymy see Dörfelt (1983*a*).

Spores 13–20 × 9–13 (16·5 ± 0·8 × 11 ± 0·6) μm, $Q = 1·5$, ovoid to short ellipsoid, adaxially applanate, thin-walled, with large refractive oil-guttules. Ultrastructurally, the wall shows a differentiated inner corium layer, similar to that of *O. japonica*, and also an electron-lucent podostratum in the myxosporial layer. A sporothecium is frequently present, forming, with the mucostratum, an encrustation of irregularly orientated, crystalline rodlets.

Specimens examined: England; Kent, Scords Wood, 6 Oct. 1968, Young; Surrey, Kew, 18 Aug. 1969, Pegler; Oxfordshire, Blenheim Park, 1969, Young; Oxfordshire, Blenheim Park, 9 Oct. 1973, Reid & Dennis. Sweden, Femsjo, Sept. 1943, Lundell. U.S.A.; N.Y. Bot. Gard., 3 Sept. 1985, Pegler.

O. RADICATA var. MARGINATA (Konr. & Maubl.) Bon & Dennis, *Documen. Mycol.* **15** (fasc. 59): 51 (1985).

Mucidula radicata forma *marginata* Konr. & Maubl., *Icon. sel. Fung.* **4**: 199 (1932).



Figs 59–66. *Oudemansiella* section Radicatae.
Fig. 59. *O. radicata*, Blenheim × 5200. Fig. 60. *O. radicata*, tetrad, × 2300. Fig. 61. *O. radicata*, attached spore, × 5200. Fig. 62. *O. radicata*, Oxfordshire, Young, × 15000. Fig. 63. *O. radicata* var. *furfuracea*, Singer V178, × 6600. Fig. 64. *O. radicata* var. *australis*, Sinnott 1971, × 4800. Fig. 65. *O. radicata* var. *australis*, Sinnott 1971, × 6000. Fig. 66. *O. radicata* var. *africana*, Ryvarden 10178, × 4800.

O. radicata var. **alba** (Dörfelt) comb.nov.
Xerula radicata var. *alba* Dörfelt, *Feddes Repert.* **93**: 61 (1983).

O. radicata var. **furfuracea** (Peck) comb.nov. (Figs 15, 63)
Collybia radicata var. *furfuracea* Peck, *Mem. New York St. Mus.* 4, **3**: 144 (1900).

Spores 14–17·5 × 10–11 (16 ± 0·8 × 10·5 ± 0·6) μm, $Q = 1·52$, ovoid to ellipsoid, adaxially applanate, with an obtusely rounded or slightly tapering apex.

Specimens examined: U.S.A.: New York, Alcove, 1892, Shear; Pennsylvania, Fayette Co., 16 Aug. 1906, Sumstone; Benson's Swamp Columbus, 16 Sept. 1947, Henning; Cyclone, 1957, Jennings; Brookston, Warren Co., 25 Sept. 1980, Henning; Massachusetts, Cambridge, June 1926, White; Amherst, 30 Aug. 1985, Pegler 3637; Conway State For., 31 Aug. 1985, Pegler 3682; Virginia, White Top Mt, 1946, Singer V178.

O. radicata var. **australis** (Dörfelt) comb.nov. (Figs 16, 64, 65)
Xerula radicata var. *australis* Dörfelt, *Feddes Repert.* **95**: 195 (1984).

Spores 13–17 × 12·5–14 (15 ± 0·8 × 10 ± 0·6) μm, $Q = 1·5$, broadly ovoid to short ellipsoid, with an obtusely rounded apex.

Specimens examined: Australia: Victoria, Benalla, Nov. 1976, Sinnott 2147, K, holotype; Mt Macedon Nat. Park, April 1976, Sinnott 1971, K, paratype.

O. radicata var. **superbiens** (Berk.) comb.nov. (Fig. 17)
Agaricus radicatus var. *superbiens* Berk. in Hooker, *Lond. Journ. Bot.* **4**: 43 (1845).
Xerula radicata var. *superbiens* (Berk.) Dörfelt, *Feddes Repert.* **94**: 559 (1983).

Spores 14·5–20 × 9–11 (17 ± 1 × 10 ± 0·6) μm, $Q = 1·7$, ellipsoid to elongate ellipsoid, adaxially applanate, with an obtusely rounded apex, thin-walled, containing large, irregular oil-guttules.

Specimen examined: Australia, Western Australia, Swan River, Drummond 119, Herb. Hooker, K, holotype.

O. radicata var. **africana** (Dörfelt) comb.nov. (Figs 18, 66)
Xerula radicata var. *africana* Dörfelt, *Feddes Repert.* **95**: 195 (1984).

Spores 19–24 × 12–14·5 (21 ± 1·4 × 13·5 ± 1·0) μm, $Q = 1·5$, ellipsoid to strongly amygdaliform to almost citriform, with an acutely tapering apex, thin-walled, with large refractive contents. This variety has very distinctive spores which are the largest within the species.

Specimens examined: Tanzania, Mt Kilimanjaro, Feb. 1973, Ryvarden 10178, K, holotype. Kenya; Rift Valley, Timboroa, April 1970, Dedan.

O. radicata var. **rubescens** (Melik-Chacatrajan) comb.nov.
O. radicata forma *rubescens* Melik-Chacatrajan, *Micol. Fitopat.* **5**: 474 (1970).
Xerula radicata var. *rubescens* (Melik-Chacatrajan) Dörfelt, *Feddes Repert.* **93**: 63 (1983).

O. radicata var. **hygrophoroides** (Singer & Clémençon) comb.nov.
O. hygrophoroides Clémençon & Singer, *Schweiz Zeitschr. Pilzk.* **49**: 124 (1971).
Xerula radicata var. *hygrophoroides* (Clémençon & Singer) Dörfelt, *Feddes Repert.* **92**: 643 (1981).

Section 5. **Dactylosporina** (Clémençon) stat.nov.
Oudemansiella subgenus *Dactylosporina* Clémençon, *Sydowia* **32**: 77 (1979).
Dactylosporina (Clémençon) Dörfelt, *Feddes Repert.* **96**: 236 (1985).

Pseudorhiza present. Spores globose, with numerous digitate outgrowths. Dermatocystidia absent. Pileipellis hymeniodermic, with some gelatinization. South America.

Type species basionym: *Tricholoma steffenii* Rick

Key to Species of Sect. Dactylosporina

1. Pileus 1·5–8·5 cm diam, umbrinous, subviscid; stipe 6·5–17 × 0·2–2·0 cm; spores 11–14 × 10–12 μm (excl. orn.), spines up to 3·5 μm long; Argentina, Bolivia, Brazil, Colombia, Venezuela . . . . . *O. steffenii*
1. Pileus 1·2–1·5 cm diam, deep brown, viscid to subviscid; stipe slender, 6–12 × 0·1–0·3 cm; spores 14–15 × 13·5–14 μm (excl. orn.), spines more than 3·5 μm long; Argentina . . . *O. macracantha*

O. STEFFENII (Rick) Singer, *Lilloa* **26**: 66 (1953). (Figs 19, 67–70)
Tricholoma steffenii Rick, *Broteria* **24**: 99 (1930).
O. echinosperma Singer, *Mycologia* **37**: 439 (1945).
Dactylosporina steffenii (Rick) Dörfelt, *Feddes Repert.* **96**: 237 (1985).

Spores 11–14 × 10–12 (12·7 ± 0·8 × 12·2 ± 0·6) μm, $Q = 1·04$ (excl. orn.), subglobose to almost globose, with large, spinose projections at maturity; adaxial surface applanate to slightly convex and the well-developed hilar appendix forms an additional spine. Young spores are smooth to verrucose and the elongate spines do not form until the later stages of sporogenesis. At maturity, the spines are uniformly dispersed over the spore, including the adaxial surface, but are separated by wide intervening spaces. The spines number 40–50 per spore, and are up to 3·5 μm long, conical, about 2·5 μm diam at the base, narrowing to 1 μm at the rounded apex. Spines are hollow, with a wall 0·3–0·4 μm thick, occasionally appearing slightly fluted, although this might be the result of collapse. Ultrastructurally, the wall teguments are comparable to those found in species of the section Xerula, with a thick coriotunica, a differentiated podostratum and a thin mucostratum. There is no evidence of any sporothecium.

Specimens examined: Bolivia: Vaca Diez Prov., Guayaramerin, 6 Mar. 1956, Singer B1612, MICH. Colombia: Valle, Buenaventura, San Joaquin, 22 April, 1968, Singer B6287, F. Ecuador: Pichilingue, 17 Feb. 1977, Cronshaw 62.

O. MACRACANTHA Singer, *Sydowia* **15**: 59 (1962).
Dactylosporina macracantha (Singer) Dörfelt, *Feddes Repert.* **96**: 237 (1985).

EXCLUDED SPECIES

O. ACULEATA Raithelh., *Hongos Argent.* **1**: 141 (1974).

On the basis of the published description, the species agrees in all characteristics with *O. steffenii*.

O. EPHIPPIUM (Fr.) Moser, *Zeitschr. Pilzk.* **19**: 10 (1955).
Agaricus ephippium Fr., *Epicrisis*: 85 (1838).

Authentic material was shown by Dörfelt (1981*b*) to be a species closely allied to *Collybia butyracea* (Bull.: Fr.) Kummer.

O. HAASIANA Raithelh., *Metrodiana* **3** (1): xxviii (1972).

Described from Argentina, the species appears to be identical with *O. canarii*.

O. KUEHNERI (Romagn.) Singer, *Sydowia* **15**: 59 (1962).
Mycenella kuehneri Romagn., *Bull. Soc. Mycol. Fr.* **56**: 65 (1940).

This small, terrestrial, mycenoid species of *Mycenella* has several structures which invite comparison with *Oudemansiella*, and Romagnesi (1940) recognized the species as intermediate between the two genera. The overall soft-putrescent habit, the non-lignicolous substratum, and the absence of any pseudorhiza are more characteristic of *Mycenella* than *Oudemansiella* section Albotomentosi, a view shared by Dörfelt (1985). Comparison was made by Singer (1975) and Boekhout (1985) between the spinose spores of *M. kuehneri* and those found in *Oudemansiella* section Dactylosporina. The *Oudemansiella* species, however, differ in having a gelatinized pileipellis and a well-developed pseudorhiza.

O. LAQUEATA (Fr.) Alessio, *Micol. Ital.* **14**: 19 (1985).
Agaricus laqueatus Fr., *Epicrisis*: 24 (1838).
Collybia laqueata (Fr.) Quél., *Enchirid.*: 27 (1886).
Armillaria laqueata (Fr.) Sacc., *Syll. Fung.* **5**: 85 (1887).

The non-lignicolous species described by Fries appears closely related to *Calocybe constricta* (Fr.) Kuehner, whilst that described and illustrated by Alessio, having small, subglobose spores, 6–7 × 5–6 μm, recalls the genus *Limacella* Earle.

O. MACROSPORA (Stev.) Horak, *New Zeal. Journ. Bot.* **9**: 434 (1971).
Limacella macrospora Stev., *Kew Bull.* **16**: 68 (1962).

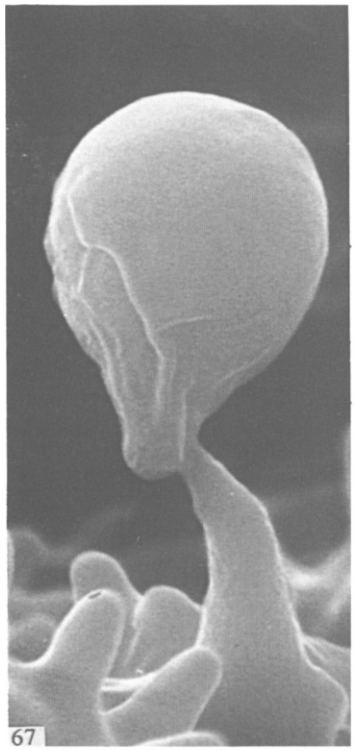
This is a species of *Amanita* Pers. with strongly amyloid spores.

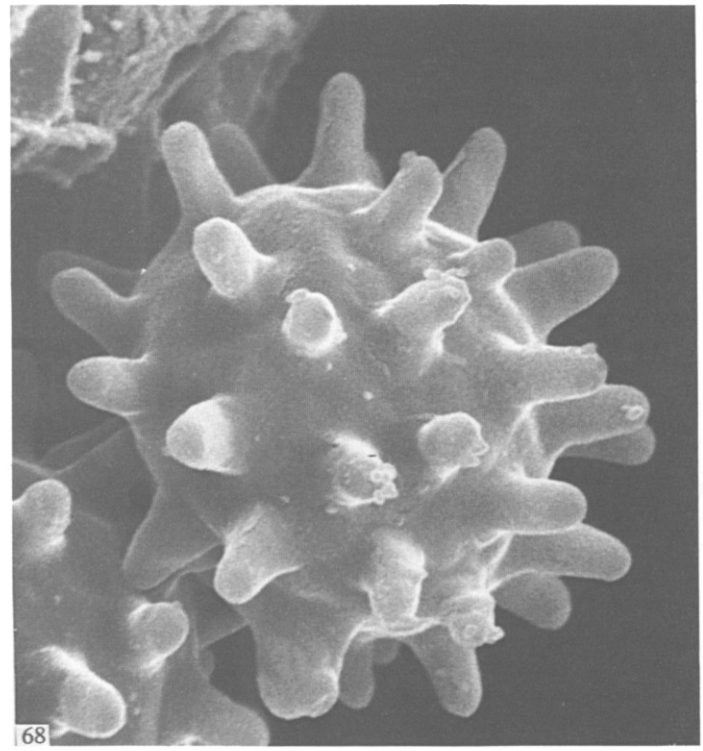
O. PILOSA (Rick) Singer, *Sydowia* **15**: 59 (1962).
Lentinus pilosus Rick, *Lilloa* **2**: 210 (1938).
Xerula pilosa (Rick) Singer, *Lilloa* **26**: 86 (1953).

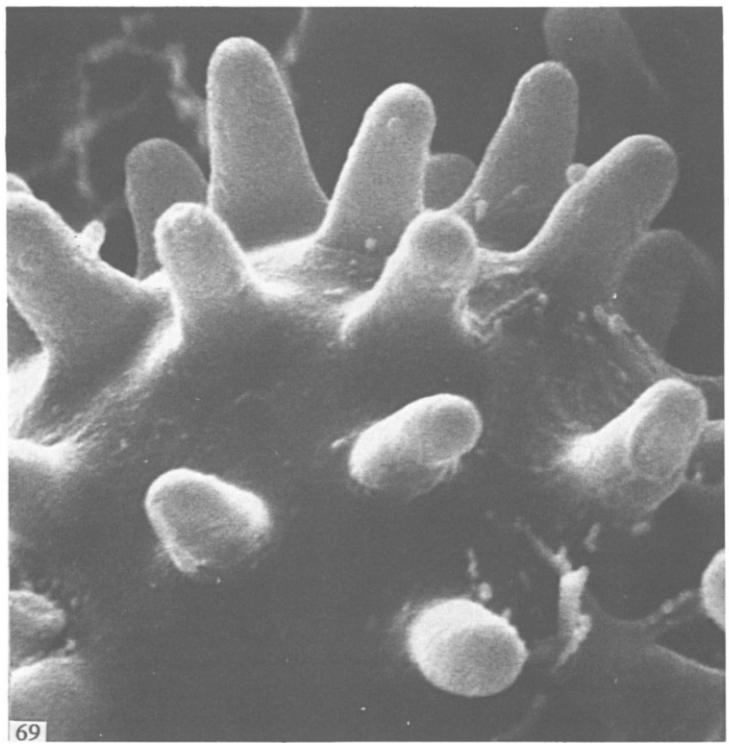
Described from Brazil, this is probably a species of *Crinipellis* Pat., see Pegler (1984) and Dörfelt (1985).

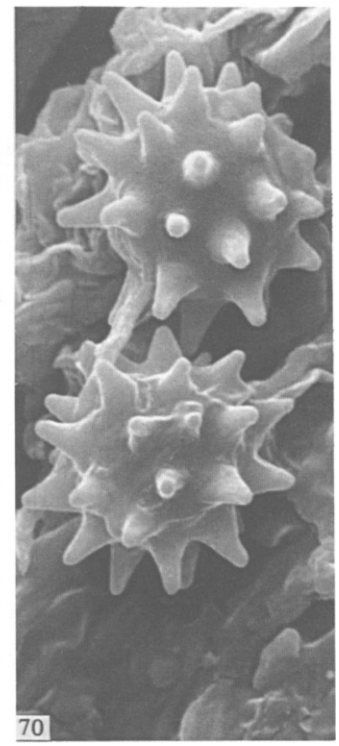
O. PLATYPHYLLA (Pers.: Fr.) Moser in Gams, *Kl. Kryptogamenfl.* **11b/2**, rev. ed. 5: 156 (1983).
Agaricus platyphyllus Pers.: Fr., *Syst. Mycol.* **1**: 117 (1821); Pers., *Obs. Mycol.* **1**: 47 (1796).
Tricholomopsis platyphylla (Pers.: Fr.) Singer, *Schweiz. Zeitschr. Pilzk.* **17**: 56 (1939).
Megacollybia platyphylla (Pers.: Fr.) Kotl. & Pouzar, *Ceská Mykol.* **26**: 220 (1972).

This species has often been associated with *Oudemansiella* since it was provisionally placed in









Figs 67–70. *Oudemansiella* section Dactylosporina, *O. steffenii* Colombia, Singer B6287.
Fig. 67. × 6400. Fig. 68. × 6000. Fig. 69. × 9000. Fig. 70. × 2350.

the genus by Moser (1955). Kotlaba & Pouzar (1972) proposed that it be accommodated in the monotypic genus *Megacollybia*, differing from *Tricholomopsis* Singer in hymeniodermic development of the pileipellis, thick-walled hyphae in the trama, and the presence of rhizomorphs with a dimitic construction. *Megacollybia* was subsequently treated as a subgenus of *Oudemansiella* by Moser (1978) and Clémençon (1979). Both authors regarded the species as the most primitive member of the genus from which all other species could be hypothetically derived. The present authors would argue against this viewpoint. The terrestrial habitat; lack of dependence on a lignicolous substratum for nutrition; reduced hymeniodermic development restricted to the centre of the pileus; the small, thin-walled spores; a complete absence of any velar layers; the dimitic hyphal system in the rhizomorphs; and a restricted north temperate distribution of the genus, collectively indicate advanced features derived from *Oudemansiella* ancestry. Dörfelt (1981) using similar characters excluded the species from *Xerula*, i.e. *Oudemansiella*, and Kuehner (1980) placed *Megacollybia* as a subgenus of *Hydropus* Kuehner ex Singer. Ultrastructurally, the spore wall does not exhibit the tegumental layering found in *Oudemansiella*, but rather a simple structure of a thick coriotunica overlain by a thin and fragmenting myxosporium.

O. PURPURASCENS Speg., *Bol. Acad. Nac. Cienc. Cordoba* **28**: 300 (1926).

The identity of this species remains unknown, and the species has never been rediscovered (Singer, 1964).

O. SUBAURANTIACA (Berk. & Br.) Petch, *Ann. Roy. Bot. Gard., Peradeniya* **4**: 391 (1910).

Marasmius subauranticus Berk. & Br., *Journ. Linn. Soc., Bot.* **14**: 36 (1873).

Marasmiellus subauranticus (Berk. & Br.) Pegler, *Kew Bull. Addit. Ser.* **12**: 109 (1986).

The gelatinous consistency, together with the caespitose habit, led Petch (1910) to transfer this species to the genus *Oudemansiella*, but Pegler (1986) has since shown it to belong in *Marasmiellus* Murr. section Tricolores Singer.

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