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THE OCCURRENCE OF ANNULATE ARMILLARIA SPECIES IN NORTHERN BRITAIN

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ABSTRACT. Full descriptions based on Scottish material are given for the lignicolous agarics *Armillaria lutea* Gillet and *A. ostoyae* (Romagnesi) Herink. The former is widespread and can act as a weak parasite but the latter is an important forest pathogen and has been collected on both native hardwoods and introduced conifers. The significance of these collections in relation to the general European distribution and ecology of the species is given. Reasons for the rejection of the names *A. bulbosa* and *A. obscura* for each species respectively are discussed. Records of *A. mellea* (Vahl: Fr.) Kummer in northern Britain, *A. borealis* Marxmüller & Korhonen, and *A. cepistipes* forma *pseudobulbosa* Romagn. & Marxmüller are briefly mentioned.

INTRODUCTION

The work of Singer (1956 et subseq.) questioned the then generally held views that *Armillaria mellea* (Vahl: Fr.) Kummer (as *Armillariella* Karsten) was a polymorphic species. Romagnesi (1970, 1973) took this concept a stage further and recognized the following distinct taxa in *Armillariella*: *A. mellea* (sensu stricto), *A. bulbosa* (Barla) Romagn., *A. ostoyae* Romagn. and *A. obscura* (Pers. ex Secretan) Romagn. Later additions to the genus were *Armillariella castulifera* Romagn. (Romagnesi, 1978), *Armillaria nigritula* P. D. Orton (Orton, 1980), and *A. borealis* Marxmüller & Korhonen (Marxmüller, 1982). *A. cepistipes* Velen. was also expanded to include the newly proposed f. *pseudobulbosa* (Romagnesi & Marxmüller, 1983). Marxmüller (1982) and Romagnesi & Marxmüller (1983) have correlated these taxa, erected on the traditional grounds of basidiomata morphology, with the five biological species recognized by Korhonen (1978) by means of mating tests performed in artificial culture.

Marked differences in pathogenicity and habitat between these species has been demonstrated (Rishbeth, 1982, 1985; Guillamin & Bertheley, 1981; Gregory, 1985) but, despite detailed studies they remain difficult to separate on purely field characters (Marxmüller, 1982; Romagnesi & Marxmüller, 1983, Watling, unpubl. data). Indeed, even cultural studies are not always as decisive as one would like. Consequently, further work on the distribution and biology of all five species is of importance to both pathologists and taxonomists. Gregory & Watling (1985) offered a full description of British collections of *Armillaria borealis,* and as a continuation of that work this paper offers a further contribution to these studies. For the first time full descriptions of British material of *A. lutea* and *A. ostoyae* are offered, supported by details of records of these species from northern Britain and by comments on the three additional native annulate *Armillaria* species.

METHODS

Cultures were made from the collections by standard aseptic techniques and were identified in mating tests by the methods described by Korhonen (1978). Collections were examined in the course of research into the agaric flora of northern Britain, and some of the cultures from

these were sent to Dr K. Korhonen of the Finnish Forest Research Institute, Helsinki for screening. These cultures were all from basidiomata and the descriptions of the taxa below are based entirely on them.

Three collections of *A. ostoyae* were all isolations made from a variety of tissues in the course of investigations by Dr S. C. Gregory, Forestry Commission, Northern Research Station, Midlothian, into *Armillaria* disease in northern British forest sites. The cultures were identified by the investigator using tester strains provided by Dr J. Rishbeth of Cambridge University, as well as single spore isolates that were collected by the author and identified using the original tester strains.

ARMILLARIA LUTEA

Romagnesi (1970) adopted *Armillaria mellea* var. *bulbosa* Barla, as *Armillariella bulbosa* (Barla) Romagn., based on the descriptions and plate in Barla (1889 p. 39, pl. 22, figs 3–7). Romagnesi characterized his material of *A. bulbosa* microscopically by the possession of numerous clamp-connections, especially at the base of the basidia, a unique feature in European species of the genus. This treatment (but as *Armillaria*) was followed by Kile & Watling (1983). However, in later correspondence with Helga Marxmüller (pers. comm.) my attention was drawn to the greater resemblance between the fungus depicted by Barla and the little known central European *Armillaria cepistipes* Velen. which has now become better understood by the activities of Antonin (1986). From specimens of similar morphology *A. cepistipes* has in fact been shown to be conspecific with Korhonen's 'species B' (Romagnesi & Marxmüller, 1983). Having re-examined the available data, and after further correspondence and discussions with Marxmüller, and Eef Arnolds and Aad Termorschuizen I agree with this conclusion.

A. mellea var. *bulbosa* Barla should be rejected as a nomen confusum (Art. 69.1), as its replacement of *A. cepistipes* Velen. for which it is an earlier name would lead to untold confusion, especially in the field of forestry.

The use of the epithet 'bulbosa', which had in fact been previously taken up by Velenovský (1927) in *Armillaria* for Barla's fungus, had become suspect from a totally different point of view: Termorschuizen & Arnolds (in ed.) have located an even earlier name—something which was to be expected as this fungus is our commonest member of the *A. mellea* complex. The name to be adopted is *A. lutea* Gillet.*

Armillaria lutea Gillet, Les Hyménomycètes, 83 (1874), Figs 1–6.

Misident.: *Armillaria bulbosa* sensu Kile & Watling (1983) and *Armillariella bulbosa* sensu Romagnesi (1970, 1973); non *Armillaria bulbosa* (Barla) Velen. (1927).

Basidiomata single, joined in pairs or threes, less frequently fasciculate and then only in small groupings, of a general ochraceous† to ochraceous

*Since this paper went to press Marxmüller (*Bull. Soc. Mycol. Fr.* 103:137–156, 1987) has introduced the new name *A. gallica* Marxmüller & Romagnesi, believing that Gillet's *A. lutea* was ambiguous.

†Colours in the descriptions follow Henderson, Orton & Watling, 1969.

pink with dark stipe-base and almost smooth to slightly scurfy pileus. *Pileus* 15–98mm, convex then plano-convex, usually remaining low, obtuse umbo, fawn or chestnut at first, clay pink or vinaceous buff towards margin, centre with small, erect fuscous black to cigar brown scales tipped with yellow or olivaceous yellow towards margin, becoming cinnamon-colour with age and in larger specimens streaked honey or dirty ochraceous yellow (G), slightly viscid when fresh and scales lost with age except at centre and these on drying becoming olivaceous or citrine, drying pale clay-pink or even ochraceous (E), sometimes distinctly wrinkled with age; margin inrolled at first and ornamented with fluffy arachnoid filaments or patches of veil, then straight or wavy and distinctly striate with dark cinnamon-colour. *Stipe* 51–98 × 13–21mm, clavate to bulbous (25–32mm base), bright yellow (luteous) at base from veil at first and roughened upwards to base of ring, yellow below ring darkening with age to become finally olivaceous grey and becoming fibrillose-striate from collapse of yellow velar material, ivory (B) above ring, striate downwards to ring, minutely punctate then darkening (C) and becoming flushed with pale salmon-colour; *ring* duplex, uppermost white, forming cortina-like connection between upper stipe and pileus-margin, lower ring, membranous-woolly, white or ivory with yellow (luteous) undersurface and edge, gradually collapsing and yellow fading, often flecked with umber scales at margin, and finally almost disappearing or leaving an annular zone; base attached in some specimens, but not always, to long, cylindric, black rhizomorphs (Fig. 6d, e). *Gills* adnate with or without tooth to subdecurrent, not decurrent, whitish then flushed with faint pinkish buff in places, becoming dirty salmon-pink, finally spotted as in *Collybia maculata*. *Flesh* white throughout, yellow in stipe base, brownish in cortex of stipe in mature specimens; *smell* faintly fragrant, fairly strong; *taste* very pleasant at first, slightly astringent then unpleasant after a minute or so mastication.

Basidiospores 7·2–8·9 × 5·6–6·7μm, broadly ellipsoid, guttulate, apparently smooth, although a few spores in any one spore-print showing some rugulosity, hyaline, pale cream-colour in mass (B), non-amyloid, with a prominent apiculus, lacking germ-pore (Fig. 1b). *Basidia* 25·5–37·8 × 6·5–8·5μm, 4-spored, with sterigmata 4–5μm long, with subtending clamp connections, hyaline or at most pale honey-coloured in aqueous solutions of alkali, usually in small fascicles (Fig. 1a, c); crassobasidia present (Fig. 2a). *Cheilocystidia* polymorphic 13–35 × 4·5–7μm, little differentiated and often in fascicles, clavate to utriform to broadly subcapitate with some slight apical modification, or even vesculose, hyaline or at most slightly honey-coloured in aqueous solutions of alkali, never septate (Fig. 2b); *pleurocystidia* apparently absent. *Pileipellis* a radially arranged cutis terminating in chains of broad cells, 39–100 × 15–30μm with apex 10–24μm, ± parallel, ± erect forming irregular, ascending then tightly adhering groups of scales; mediopellis of parallel to subparallel hyphae, 5–7·5μm, with vacuolar pigment, seated on a hyaline layer of anastomosing hyphae, neither layer gelatinized except when fully mature (Figs 5a, b, 6a). *Stipitipellis* of filamentous, often thickened cylindric hyphae, 3·3–4·5μm broad, overlying hyphae 3·5–7·5μm broad covered in filamentous fragments of velar debris particularly at the

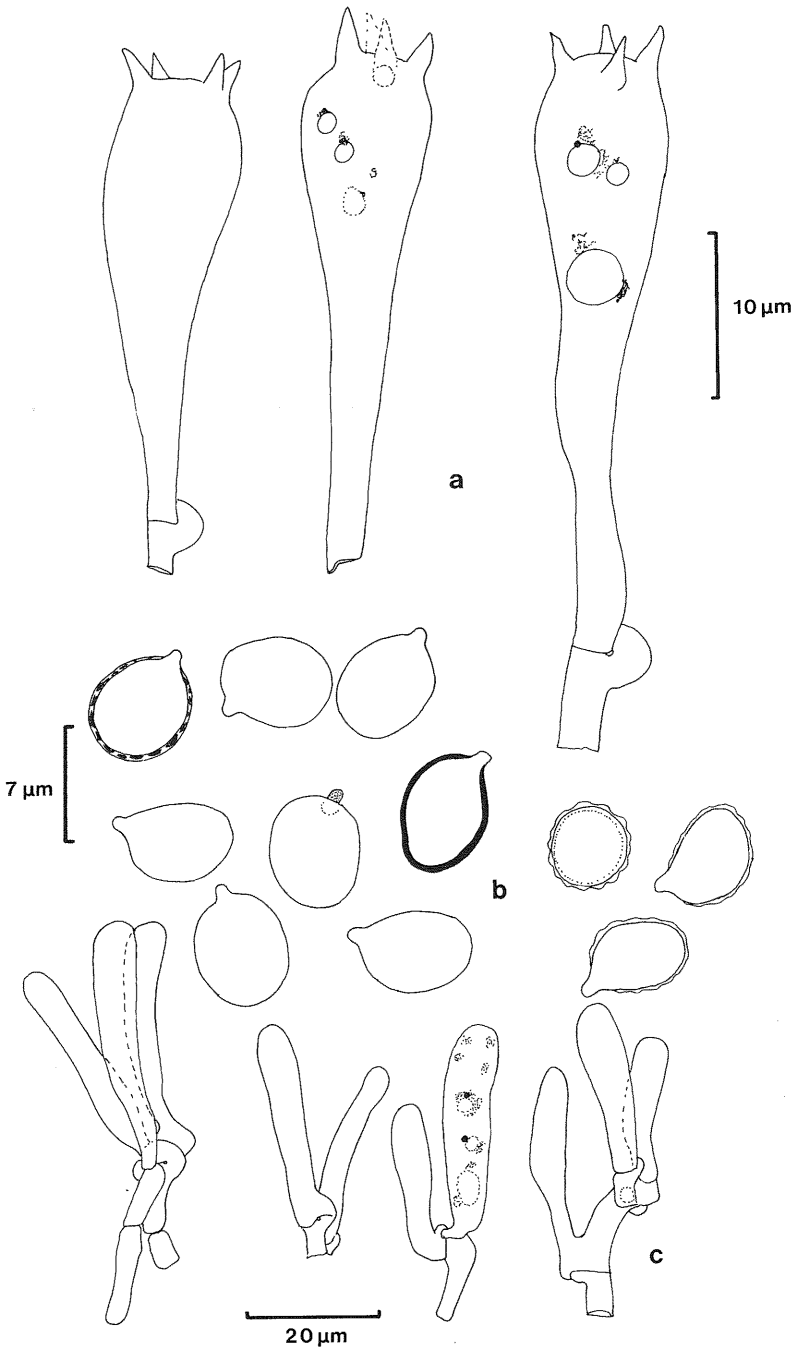


FIG. 1. *Armillaria lutea*. a, basidia with basal clamp-connections; b, basidiospores, three showing irregular surface after treatment with concentrated alkali; c, fascicles of basidioles. All from *Watling* 11507.

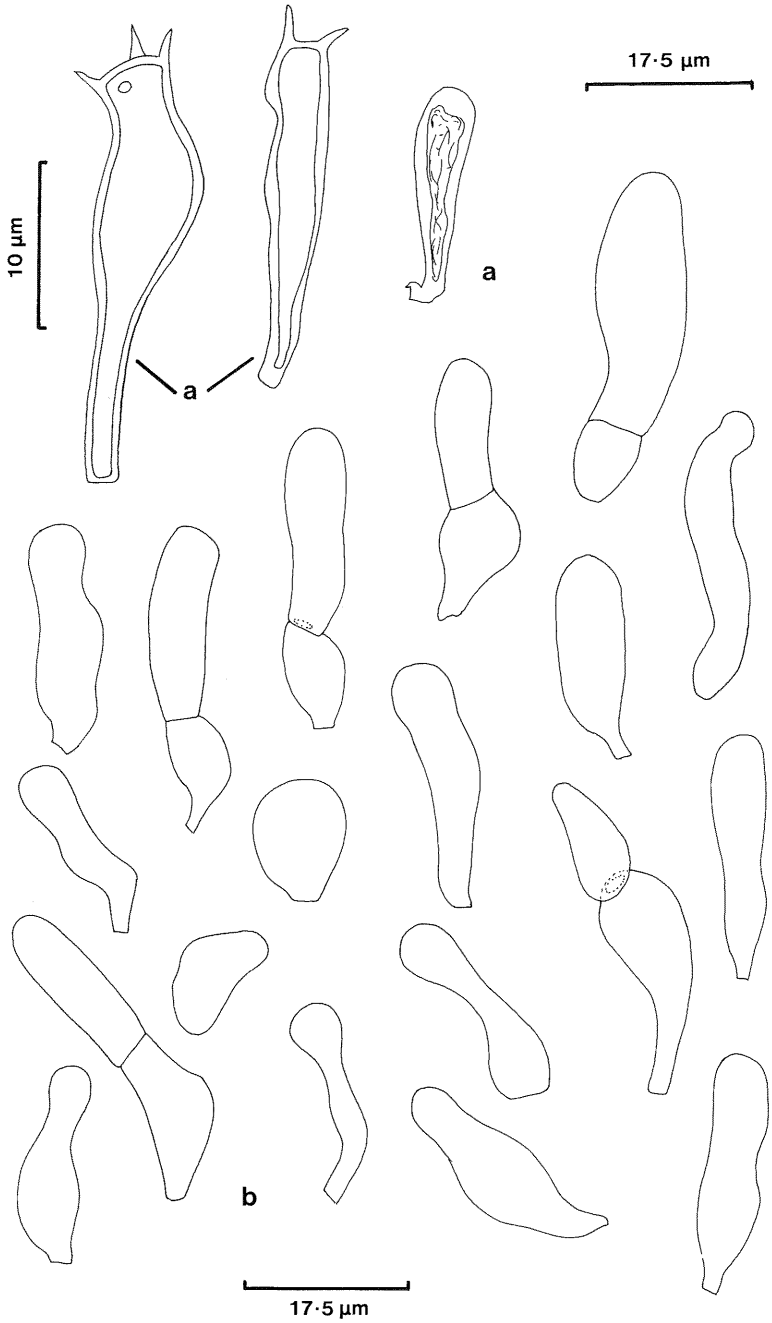


FIG. 2. *Armillaria lutea*. a, crassobasidia; b, cheilocystidia. From *Watling* 11507.

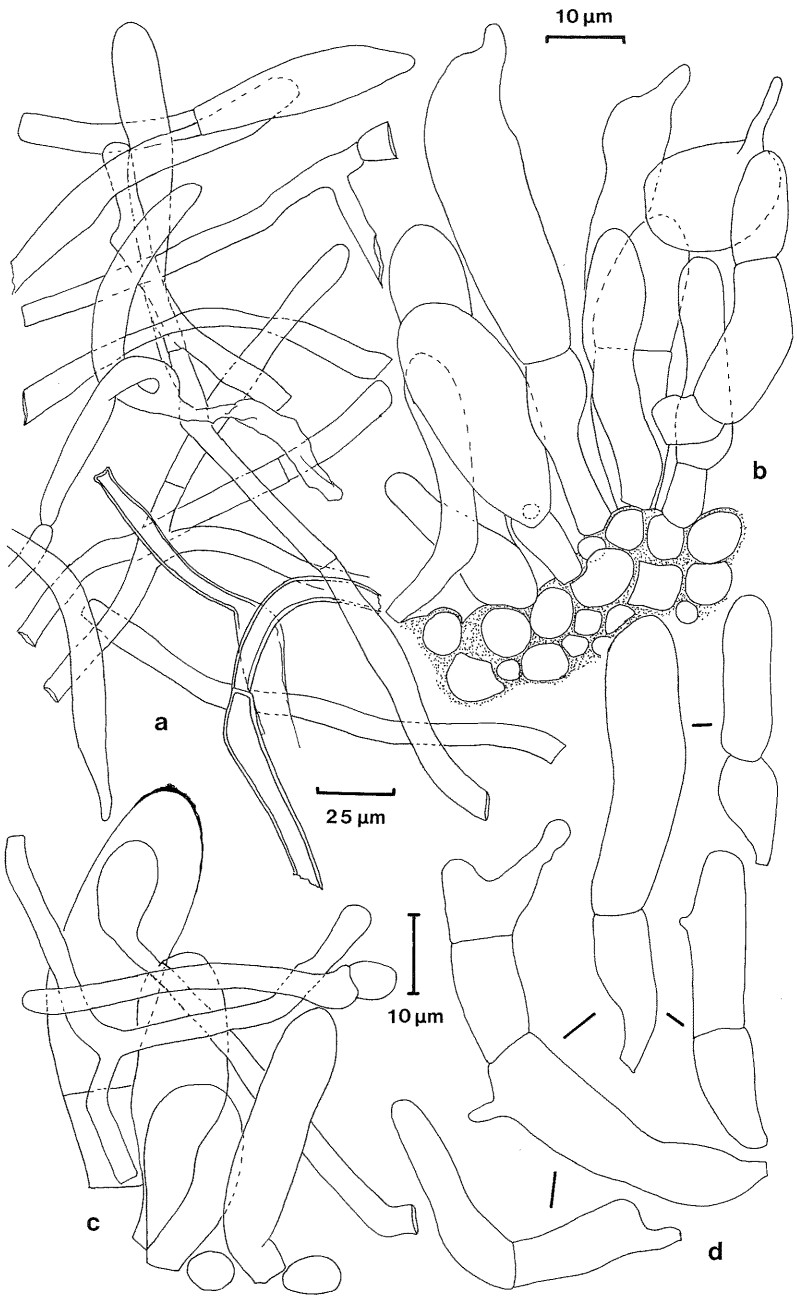


FIG. 3. *Armillaria lutea*. a, veil at base of stipe; b, stipe-surface with differentiated cells; c, velar elements covering caulocystidia; d, caulocystidia. All from *Watling* 11507.

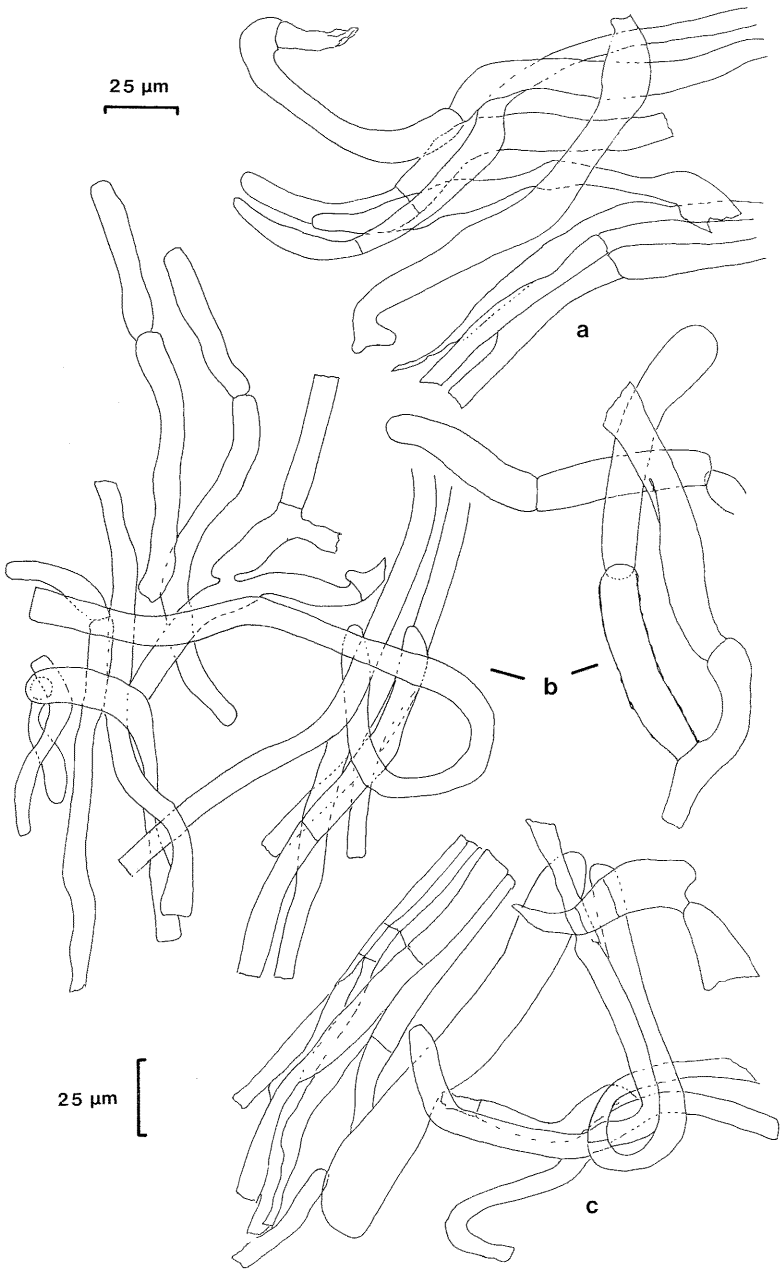


FIG. 4. *Armillaria lutea*. Velar structures: a, velar elements from stipe-apex; b, velar elements attached to gill margin; c, velar elements at margin of annulus. From *Watling* 11507.

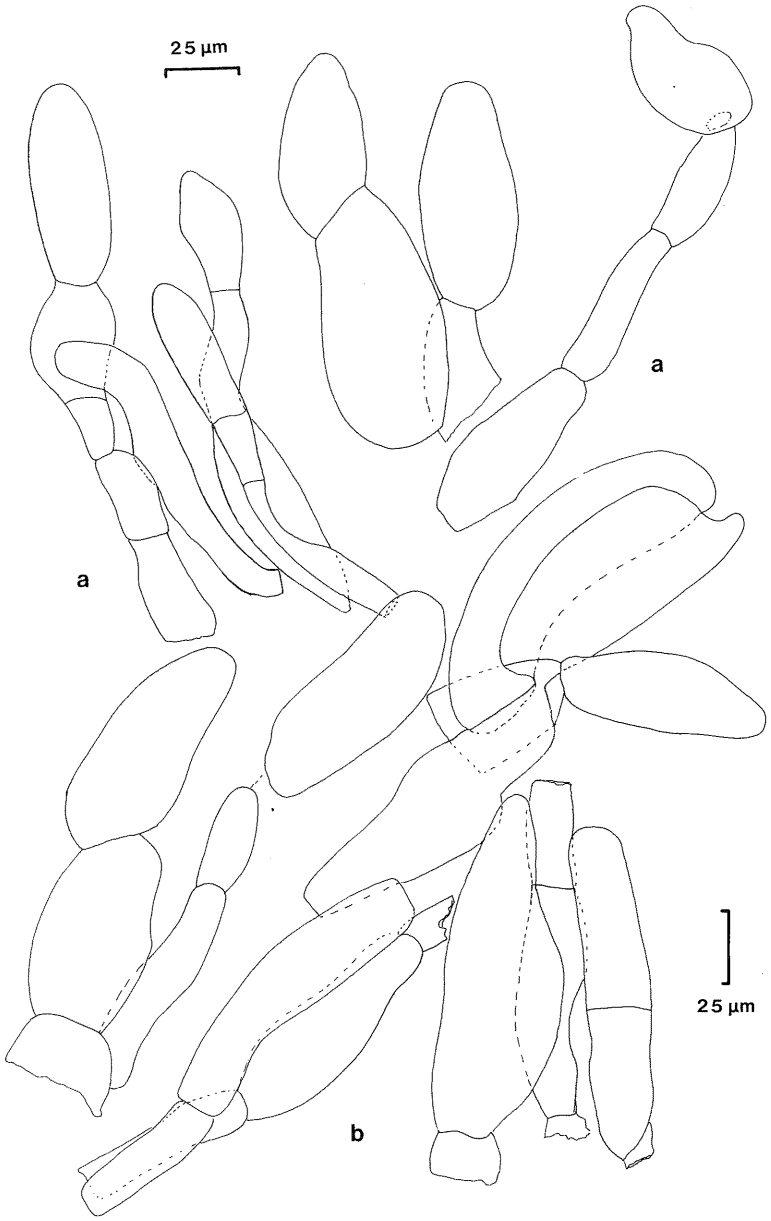


FIG. 5. *Armillaria lutea*. a, upward directed hyphae of suprapellis; b, scales composed of fragmented chains of suprapellis. From *Watling* 11507.

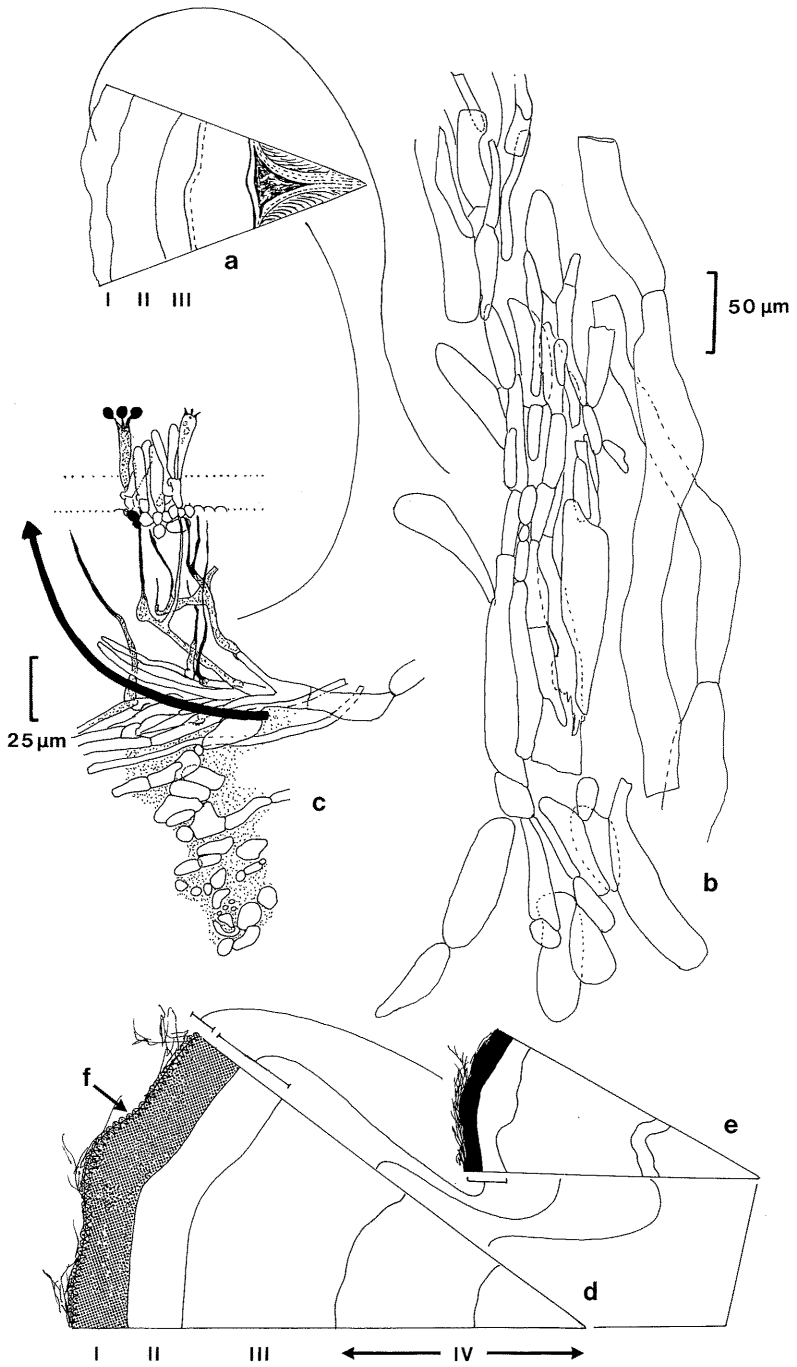


FIG. 6. *Armillaria lutea*. a, section of pileipellis with basal part of hymenophoral trama; b, pileipellis in mature basidiome showing remnants of scales; c, hymenophoral trama of hymenium showing bilateral and divergent nature; d & e, TS of lower part of stipe (d) and of rhizomorph (e) showing similar zonation consisting of I suprapellis, II mediopellis, III subpellis and IV medulla, I–III = rind; f, stipitipellis composed of palisade of cystidiform cells. All from *Watling* 11507.

stipe base and irregularly upwards (Fig. 3b). *Caulocystidia* as variable as those found on the gill margin and similar in shape although usually more often vesiculose 30–67 × 33·5μm, sometimes septate 84 × 20μm with lower cell 15·5μm broad (Fig. 3d). *Velar material* of ring composed of ± thin-walled, filamentous flexuous to cylindric, intertwined often anastomosing hyphae on upper surface 48–67 × 9·5–18μm which form broader penultimate and terminal cells 66–140 × 9·5–21·5μm, often tapering to 6μm broad at tip and similar to those in suprapellis and peripheral areas of ring. Lower surface of ring composed of hyphae from 66μm long × 12–25μm connecting with hyaline hyphae clothing the stipe 9·5–15·5μm broad (Figs 3a–c, 4a–c). Velar remnants on pileus 18–26·5μm broad and veil half-way down stipe 5–12μm broad and up to 132μm long with lowest hyphae 10–12μm broad. *Hymenophoral trama* very slightly bilateral with gelatinized hyaline lateral strata and slightly darker (pale honey-coloured) medio-stratum; lateral strata quite narrow, only a little broader than the honey-coloured, highly branched hymenial zone (hymenium/subhymenium hyphae 3μm broad); mediostratum up to twice as broad as lateral strata (Fig. 6a, c). *Context* of hyaline, anastomosing, only slightly coloured hyphae which separate to produce a floccose texture in the central zones, more compacted and appearing cellular between the gills immediately above the hymenial layer.

Habitat: solitary or scattered in small groups, often in loose tufts of a few basidiomes, not necessarily directly on wood, although from colonizing rhizomorphs attached to wood or from buried wood.

Collections examined: Scotland: Midlothian, Royal Botanic Garden, Edinburgh, on soil amongst grass and rose bushes in Rose lawn, 1 x 1975, *Watling* 11507 (E); ibid., 30 x 1972, *Watling* 9183 (E); ibid., 6 xi 1973, *Watling* 10089 (E); ibid., 9 x 1975, *Watling* 11313 (E); ibid., 28 ix 1977, *Watling* 12404 (E); Royal Botanic Garden, Edinburgh, in Azalea lawn, 30 x 1973, *Watling* 10101 (E); ibid., 16 x 1974, *Watling* 11194 (E); Hermitage of Braid, Edinburgh, on *Fagus,* 13 x 1973, *Watling* 9887 (E); Bush Estate near Roslin, on old fallen trunk, 27 ix 1979, *Watling* 13384 (E). Dunbartonshire, Shore Wood, Loch Lomond, on *Quercus,* 10 x 1979, *Watling* 13488 (E). Perthshire, near Acarn, Loch Tay, on ground under *Picea,* 17 x 1979, legit D. Taylor, *Watling* 13481 (E).

A. lutea produces copious rhizomorphs which permeate the soil around old trunks and stumps and infected plants, and spread under and over bark to form a reticulate or sheet-like structure. It is common in gardens and parks where it may attack plants in a debilitated state having suffered from cultivation damage, predisposed from earlier water-logging or drought etc. This is reported to be the species involved in the *Galeola* (Orchidaceae) mycorrhizal relationship described by Hamada (1940); see Rishbeth, 1985. It is probably the species most commonly associated with the aborting *Entoloma abortivum* (Berk. & Curt.) Donk in eastern North America (Watling, 1974).

A. lutea has not fructified in pure culture, although cultures can be readily obtained which produce copious rhizomorphs. Fresh collections suggest that *A. lutea* is both metavelangiocarpic and stipitocarpic with the outermost layers of the pileus forming the characteristic scales, whilst the

development around the gills forms a cortinate veil which splits to form a collapsed white ring bordered and ornamented below with cells similar to those on the pileus surface. This type of development explains why caulocystidia are found over the major part of the stipe but, unlike *Conocybe,* their morphology does not assist in separating closely related taxa.

In general, with the use of either phase contrast microscopy or staining techniques (e.g. phloxine in ammoniacal solutions, or erythrosin) the irregular nature of the outer wall of the basidiospore in this species can be demonstrated, and is confirmed by transmission electron microscope studies. The basidiospores of typical *A. lutea* and its grey form (see below) are similar in all respects; they are the most ornamented of all British taxa within the genus.

A description of a collection, completely interfertile with *A. lutea* but lacking the yellow ring is offered:

Pileus 22–100mm broad, convex then plano-convex, commencing milky-coffee colour covered in erect to suberect hazel to sepia-coloured scales which are denser at the disc, concentrically arranged, the centre a dark sepia colour, dirty rust tawny at margin covered in white fibrils from cortina, striate only with age, scales becoming flattened and easily lost, depressed and few if any finally at margin, pale sienna to deep honey with age (as in *Galerina*) although retaining sepia disc, drying out paler honey or where protected clay-pink, finally very pale buff, at first almost uniformly scabrous sepia and deep rusty tawny at very margin at start of expansion and cortina breaking. *Stem* pale yellowish (F) at most but only at very base and retained into maturity at very base as H, very pale sienna to deep honey-colour below a white fibrillose surface at first, when rubbed pinkish cinnamon, covered in scurfy sepia or hazel woolly scales in concentric rings which continue upwards and give the under surface of the ring a hyena-spotted appearance; ring white stretching to margin as white cortina but on lower surface dirty sepia spotted, finally leaving a uniform weft (like an old dirty cob-web) below or as sepia to hazel floccules at margin perhaps at most a reddish honey edge to margin. *Gills* with tooth running to top of ring, pale yellowish (D) at first then with pinkish rust margin or finally pale C or B or even paler, with maturity spotted rusty as in *Collybia maculata. Flesh* in pileus buff or with hint of pinkish buff, darker line over the gills and with a slight yellowish flush at apex of stipe with maturity; taste very slowly soapy but strong and then disappearing.

Basidiospores pale cream-colour in mass (B–C, Pearson; Blanchâtre–Crême blanchâtre, Romagnesi). Other microscopic details as for typical form.

Habitat: on old fallen trunk, Bush Estate, near Roslin, Midlothian, 27 ix 1979, *Watling* 13385—as *A. polymyces* (E).

It is interesting to note that the above collection, which was originally identified as *Armillariella polymyces* (Secretan) Singer & Clemençon because of the lack of yellow colours in the veil, darkening gills and the overall greyed appearance, was fully compatible in infertility tests with Korhonen's 'sp. E' i.e. *A. lutea.*

The present study does not support an earlier suggestion that Schaeffer's plate of *Agaricus obscurus* might be identified as this non-yellowing form of *A. lutea* (Watling, Kile & Gregory, 1982). For further discussion on this coloured illustration, and *Agaricus polimyces* (a variant spelling) see below under *A. ostoyae*.

ARMILLARIA OSTOYAE

Armillaria ostoyae (Romagn.) Herink was originally described by Romagnesi (1970 as *Armillariella*) when he investigated the aggregate nature of *A. mellea* (Vahl.: Fr.) Kummer; at the same time he recognized '*Armillariella obscura* (Pers. ex Secretan) Romagnesi', separating the two mainly on ecology and prominence of pileal scales. Three years later Romagnesi (1973) offered a second description of *A. obscura*.

Korhonen (1978) suggested that *Armillaria ostoyae* (as *Armillariella ostoyae* Romagn.) was identical with his 'species C', and this was confirmed by Rishbeth (1982) based on cultural studies using British isolates. The results from the present study and the observations made by Marxmüller (1982) support this conclusion. Further, the latter author in collaboration with Printz suggested that *A. ostoyae* and *A. obscura* are one and the same taxon (Marxmüller & Printz, 1982). Based on his interpretation of the data available, the present author supports Termorsuizen & Arnolds (in ed.) in adopting *A. ostoyae* to cover Korhonen's 'species C'.

If as Romagnesi (in Romagnesi & Marxmüller, 1983) now insists, his interpretation of *A. obscura* and his new species *A. ostoyae* are one and the same then the use of the earlier epithet *obscura* to cover both names needs to be explored.

AGARICUS OBSCURUS PERS.

Agaricus obscurus Pers. was introduced in '*Agaricus* sectio tertia *Gymnopus*' by Persoon (1801, p. 347) for the fungus *Inocybe obscura* Gillet which has generally been misapplied for *I. phaecomis* var. *major* (S. Petersen) Kuyper (Kuyper, 1986). *Ag. obscurus* Pers. was taken up by Fries (1838, p. 173 and 1863, p. 300) and this agaric was well known in Britain (e.g. Berkeley & Broome, 1854; as no. 682 *Agaricus* (*Hebeloma*)) and figured by Saunders & Smith (1871, t. 21). Thus Persoon's name cannot be attached to an *Armillaria*, indeed according to the current ICBN (Voss, 1983) *Ag. obscurus* Pers. (1801) is a later homonym of *Ag. obscurus* Schaeffer (1774); neither of these names were sanctioned by Fries (1821) (Art. 13. 1d).

Secretan (1833) also used the epithet 'obscurus' for a species of *Armillaria*. The validity and identity of Schaeffer and Secretan's names should therefore be explored to see if they refer to identical agarics and whether if one or other, or both, refer to *A. ostoyae*.

AGARICUS OBSCURUS SCHAEFFER

Agaricus obscurus Schaeffer (1774) is based on plate 74 and its accompanying description in Schaeffer (1762). The plate (reproduced here as Plate 1) depicts eight figures: *fig. 1* shows a primordium; *fig. 2* a

slightly older basidiome but with ring intact; *fig. 3* a more opened pileus with pink tints to the gills and ring; *fig. 4* a pair of maturing basidioma; *fig. 5* one fully expanded pileus with obtuse central umbo and concentrically arranged scales; *fig. 6* an (exannulate) section depicting a hollow stipe and adnato-emarginate gills tinged brownish at their bases; *fig. 7* a spore-print and, *fig. 8* three basidiospores.

What is most distinctive in the plate is that the rings lack any ornament and the stipes are quite smooth. *A. ostoyae* as defined by Romagnesi (1970) is very distinct in the field and recognized by the chocolate brown spike-like scales. Of all the European species of *Armillaria* probably *A. mellea* and *A. ostoyae* are the two which can be identified most correctly from macroscopic and microscopic characters, without resorting to cultural techniques. Even allowing for artistic licence the fungus depicted in Schaeffer's plate and *A. ostoyae* are certainly not the same.

This plate is stated by Fries (1821 et subseq.) to be the same as his *Ag. melleus,* as is the description of *Ag. polimyces* Pers. but it is almost lost amongst the many other epithets introduced by Batsch, Bolton, Bulliard, Withering etc., which are all placed in synonymy by Fries. Fries clearly had a wide concept for *Ag. melleus,* a concept which has linked generations of mycologists until the present day. Schaeffer's plate does not represent *Armillaria mellea* (Vahl: Fr.) Kummer as accepted in its present, restricted sense. Fries (1838) later accepted *A. laricinus* Bolton as rather different and, as in some other taxa, perhaps modified his concept a little with age; *Ag. polymyces* was still included however, in this concept.

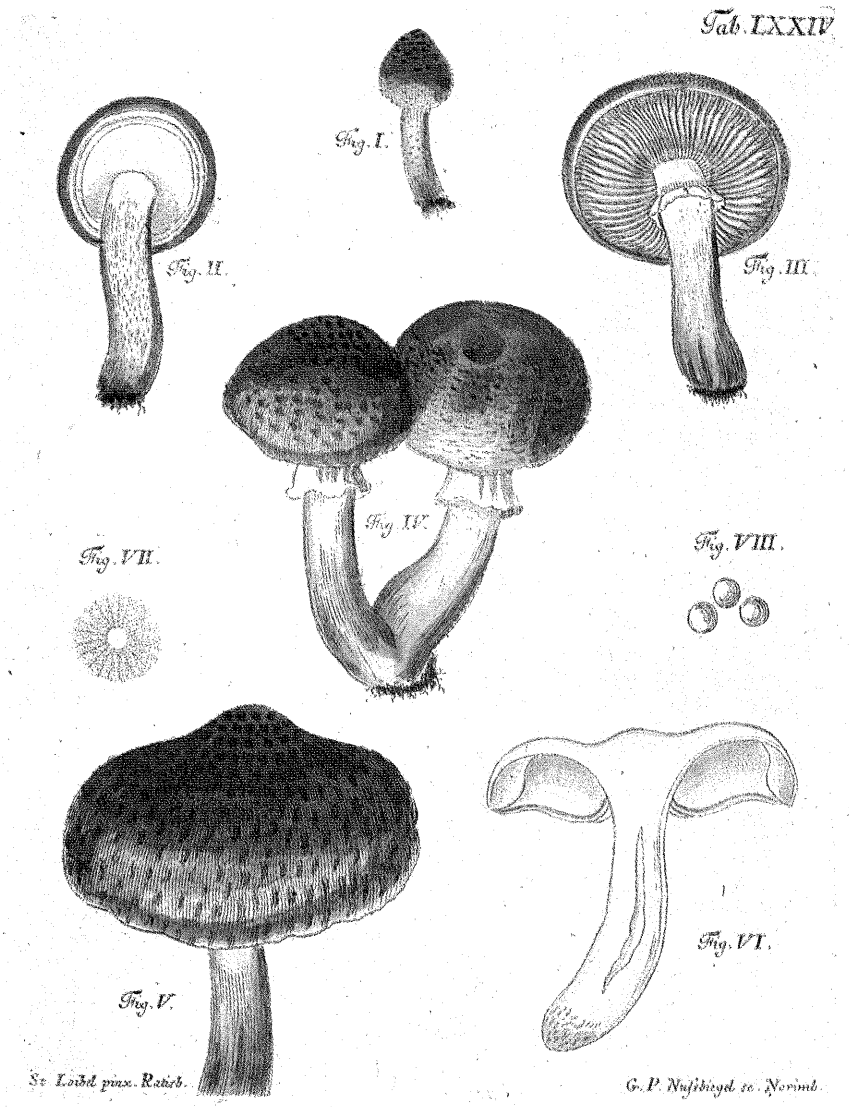
Schaeffer's plate 74 does not agree with any species of *Armillaria* known to the author, indeed it may not even represent a species of *Armillaria*.

Roll-Hansen (1985) mistakenly believed that *Ag. obscurus* was first validated by Persoon in his commentary to Schaeffer's plates (Persoon, 1800), and overlooked the actual validation by Schaeffer (1774).

AGARICUS POLYMYCES PERS.

What is *Agaricus polymyces*? This name was introduced by Persoon (1797) and linked then, and four years later (Persoon, 1801) with '*Ag. melleus*. Fl. dan., t. 1013 and Bolt. fung. t. 141. *Ag. congregatus*. Bolt. fung. t. 140. *Ag. fuscopallidus*. Bolt. l.c. t. 136 (varietas). *Ag. annularius* Bull. herb. t. 540 f. 3. *Ag. stipitis* Sowerby engl. fung. t. 101. *Ag. cumulatus*. Wither. bot. arrang. ed. 3. v. 4 p. 164', in short the whole gamut of members of the *Armillaria mellea* complex. It is clearly a superfluous name. Despite this, Singer & Clemençon (1972) took up the epithet (as *Armillariella polymyces*) when they described material from Germany and Switzerland. These authors wrote 'this is precisely the species described by Secretan from a place only a few kilometres from the C5433 under the name *Agaricus polymices* (sic), with reference to Persoon synopsis p. 269 which at least partly belongs here as does Letellier pl. 8, fig. 70'. It was Secretan in fact who restricted *A. polymyces* to one definite species but this was not *A. ostoyae*!

Gray combined the name *Ag. polymyces* in *Lepiota* (1821) following Persoon, as Lange did over 100 years later (1915) for *Ag. melleus,* but



Lepiota (a). obscurus. ? Schäff
— polymyces P. Disp. Meth. Fung.

Gray does not contribute to our understanding of the problem as there is no doubt, judging from the figures he quotes, that he simply used the epithet 'polymyces' in the same way Fries used 'melleus', and therefore this covered *Ag. obscurus* Schaeffer in addition to other taxa now considered distinct.

SECRETAN'S TREATMENT

It was Secretan (1833) who first carefully separated out the various taxa within the *Ag. melleus* complex, viz. four species with several varieties. *Ag. polymices* he characterized by Bulliard's plate 540 fig. 3 (*Ag. annularis*) and Bolton's plate 140 (*Ag. congregatus*). Under *Ag. obscurus* he included Persoon's observations to the entry for *Ag. polymyces* (Persoon, 1801, p. 271), Bulliard's plate 543 (*Ag. annularis*) and Schaeffer's plate of *Ag. obscurus,* thus linking Schaeffer's plate 74 and Persoon. The other species of *Armillaria* he dealt with were *Ag. annularius* based on Bolton t. 141 (*Ag. melleus*), and *A. annularius luteus* based on Sowerby t. 101 (*Ag. stipitis*?); the last probably refers to *Armillaria lutea* Gillet. Secretan's description of *Ag. obscurus* does not refer to *Ag. ostoyae* because of the discrepancies in the characters mentioned, particularly those of the ring.

It should be noted that species names in Secretan (1833) are considered not validly published because Secretan did not consistently use binomials in that work (Art. 23.6c).

'ARMILLARIELLA OBSCURA' OF ROMAGNESI

It was in the sense of Secretan (1833, p. 47) that Romagnesi (1970, 1973) took up *Ag. obscurus* as '*Armillariella obscura* (Pers. ex Secr.) Romagn. n.c.' The cited basionym was '*Ag. polymyces obscurus* Pers. *Syn. f.,* p. 271, obs.', but this name does not appear anywhere in Persoon (1801) and Romagnesi's combination is invalid (Art. 33.2). If a very broad interpretation is taken of Art. 33.2 and Romagnesi is considered to have made a bibliographical error of citation, then his combination would have to be considered to be based on *Ag. obscurus* Schaeffer. As noted above, species names published in Secretan (1833) are invalid. Even if they were not, Secretan did not introduce a new name '*Agaricus obscurus* Secr.' for he included 'Schaeffer, t. 74. A. obscurus.' in synonymy. The fact that Secretan's description of *Ag. obscurus* may well not belong to the species depicted by Schaeffer is irrelevant for the purposes of nomenclature.

PLATE 1. Plate 74 [*Agaricus obscurus* Schaeffer] from the 2nd edition (1800) of Schaeffer's *Fungorum qui in Bavaria et Palatinatu* . . . The plates of this edition are identical to those of the original, but have an added commentary by Persoon (see Stafleu & Cowan, 1985). The Edinburgh copy, purchased in 1903, is annotated by the Rev. M. J. Berkeley. Although the hand-written comments below plate 74 are not signed, those with plate 41 are, and have been confirmed as Berkeley's by Dr S. Buczacki (pers. comm.). The plate of *Ag. obscurus* is annotated in pencil: 'Lepiota (A) obscurus ?Schaeff.—polymyces P. Disp. Meth. Fung.'. The first part is by Berkeley, the second part, 'polymyces . . .', is in a different (unidentified) hand.

Note the lack of scales on ring-margin and stipe.

Singer & Clemençon (1972) do not consider that their interpretation of *Armillariella polymyces* is the same as *A. obscura* sensu Romagnesi: on the contrary Singer (in Singer & Clemençon, 1972) indicates that Romagnesi's *A. obscura* is the same as *Armillariella montagnei* var. *umbrinobrunnea* Singer, a fungus first described from Patagonia, S America (Singer, 1956) but since found at Femsjö, Sweden (Singer, 1969). No cultural studies alas were carried out to see if their *A. polymyces* and *A. ostoyae* (i.e. Korhonen's sp. 'C'), and the Femsjö collection were interfertile. If this were true then *montagnei* Singer (1956) or '*umbrinobrunnea*' might be available for use as a specific epithet, but from results with Australian and European taxa, e.g. *A. mellea* s. str. and *A. luteobubalina* Kile & Watling, superficial similarities between taxa might be misleading if other microscopic differences and genetic isolation are not taken into account (Watling, unpubl. data; Kile, pers. comm.; Mohamhed, pers. comm.). It would be hasty to adopt the name of a S American taxon for a European one. Only where it could be proved the fungus had been originally introduced into S America in the first instance would it be possibly acceptable with our present knowledge.

What, then, do we call '*Armillaria* sp. C' of Korhonen? *Agaricus obscurus* Pers. is not an *Armillaria,* and *Ag. obscurus* Schaeffer is of uncertain identity and may not even be an *Armillaria.* There are also no interfertility studies and insufficient microscopical data to countenance the use of *Armillariella montagnei* Singer or its var. *umbrinobrunnea* Singer. Thus, it is proposed herewith to recommend the use of *Armillaria ostoyae* which is based on extant type material, a full macroscopic and microscopic description, figures and a coloured photograph, and is supported by cultural information from Korhonen's studies of collections identified as *A. ostoyae* by Romagnesi.

A summary of interpretations of some early epithets associated with *Armillaria mellea* s. lat. and '*A. obscurus*' is presented in Table 1.

Armillaria ostoyae (Romagnesi) Herink in Hasek, J. (ed.) Sympozium o václavky obecné, September 1972; Taxónomie Václavky obecné *Armillaria mellea* (Vahl ex Fr.) Kummer Lesnicka fakulta VSZ Brno. p. 42 (1972). Figs 7, 8.

Basionym: *Armillariella ostoyae* Romagnesi in Bull. Soc. Mycol. Fr. 86:265 (1970).

Misident.: *Armillariella obscura* (Pers. ex Secretan) Romagnesi s. Romagnesi, 1970 & 1973; auct. pl. *Armillaria obscura* (Schaeffer) Bon s. Bon in Documents Mycol. 15(60):38, 1985.

Basidiomata fasciculate, of a general pinkish to cinnamon brown with vandyke or umber scales (Fig. 7a, b). *Pileus* 35–55mm, convex or rounded, expanding to become broadly obtuse, or with a slight umbo, to dome-shaped, even at maturity retaining marginal frill, roughened throughout at first then with dark fibrils, closely packed vandyke to umber brown scales at disc and rings of dark vandyke or umber brown scales on buff background towards margin, scales detersile especially with age or handling, finally with only a few scales retained at disc, and then these

TABLE 1

Summary of various interpretations of some early epithets associated with *Armillaria mellea* s. lat.

Epithet/Author	Date/pagination	Classic interpretation	Present interpretation
obscurus			
Schaeffer	1762 pl. 74, 1774		Nomen confusum
Villars	1789: 1015	*Agaricus* (*Lepiota*) *clypeolarius* fide Fries, 1821:21	*Lepiota clypeolaria* (Bull.: Fr.) Kummer
Persoon	1801: 347	*Agaricus* (*Gymnopus*) *obscurus*	*Inocybe obscura* Gillet =*I. phaeocomis* var. *major* (S. Petersen) Kuyper
Schumacher	1803: 279	*Agaricus* (*Pratella*) *udus* fide Fries, 1821: 292	*Hypholoma udum* (Pers.: Fr.) Kühner
Secretan	1833: 47	[Bulliard *Ag. annularis* pl. 543 & Schaeffer pl. 74] *Agaricus melleus* fide Fries, 1821: 30*	Nomen superfluum (Art. 63)
Fries	1838: 173	*Agaricus* (*Inocybe*) *obscurus*	*Inocybe obscura* Gillet =*I. phaeocomis* var. *major* (S. Petersen) Kuyper
Romagnesi	1970 & 1973	as *Armillariella obscura* (Pers. ex Secretan) Romagn.	*Armillaria ostoyae* Romagn.
polymyces (variant spelling polimyces)			
Persoon	1797: 19	*Agaricus obscurus* Schaeffer = *Ag. melleus* fide Fries 1821: 30*	Nomen superfluum (Art. 63)
Gray	1821: 603	*Ag. melleus* fide Fries, 1821: 30*	
Secretan	1833: 312	[Bolton *Ag. congregatus* pl. 140 & Bulliard pl. 540, fig. 3] *A. polymyces* s. Singer & Clemençon, 1972	Nomen invalidum (Art. 23. 6c)
calamistratus			
Fries	1821: 256	*Agaricus* (*Dermocybe*) *calamistratus*	*Inocybe calamistrata* (Fr.) Gillet
Weinmann	1836: 396	*Agaricus obscurus* fide Fries, 1838: 173	*Inocybe obscura* Gillet =*I. phaeocomis* var. *major* (S. Petersen) Kuyper

*Broad concept.

suberect, and a scattering of brownish scales over marginal half, becoming blotchy with age and water-soaked (expallent/hygrophanous), pinkish clay or buff-pink increasingly showing through on expanding then cinnamon-buff outwards from dark brown centre. *Stipe* annulate, equal or hardly swollen, fibrous 50–90 × 4–10·5mm, hollow, little or no olivaceuous tints at base, white at apex at first clay-pink below but half-way up or from base up covered in small vandyke brown scales tipping white woolly floccules arranged in concentric patterns, darkening with age from base upwards, almost smooth except for floccules, scales at centre more pointed than those at base, recurved (cockatoo-like); *ring* membranous, white beneath with a line of brown, angular scales at junction with stipe, and brown line around edge, becoming more fuliginous and spotted with

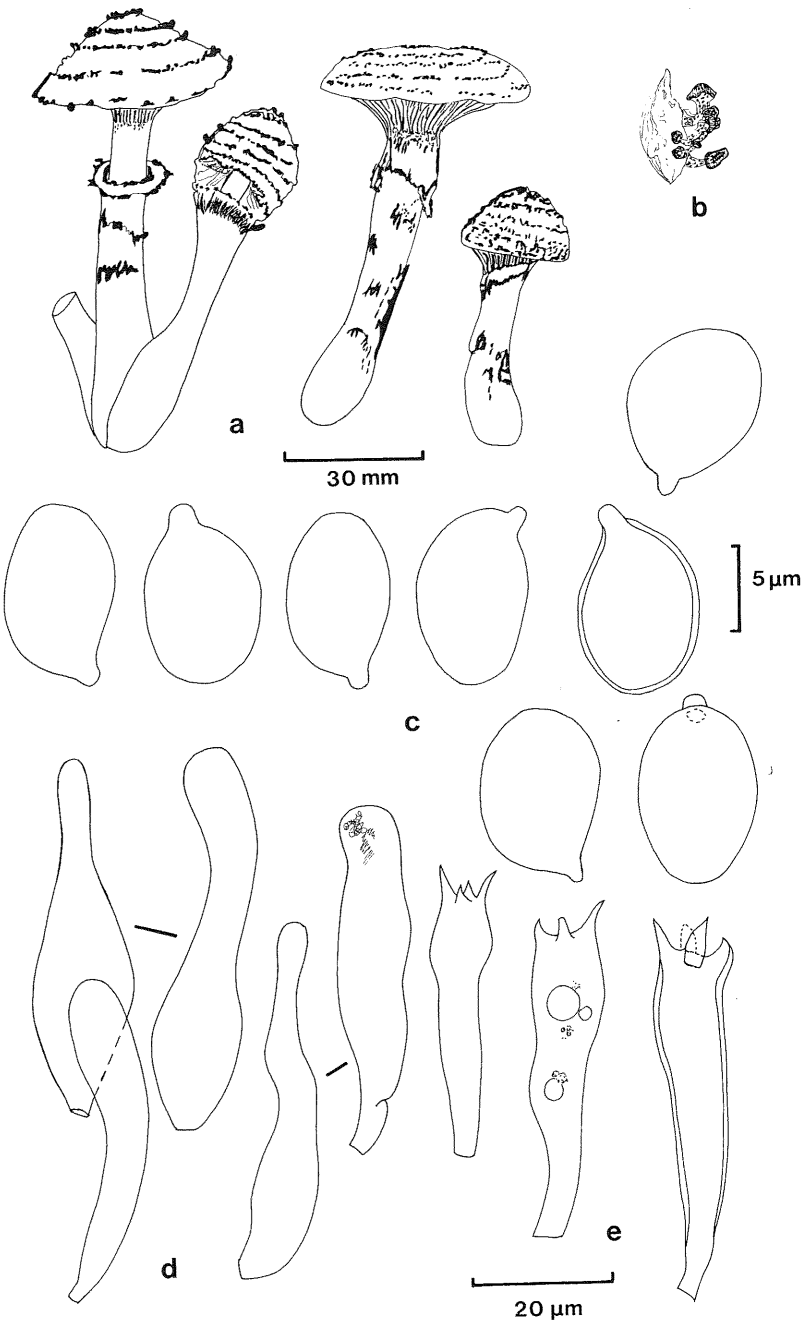


FIG. 7. *Armillaria ostoyae*. a, habit sketch with group of primordia (b); c, basidiospores; d, cheilocystidia; e, basidia—one crassobasidium. All from *Watling* 11509.

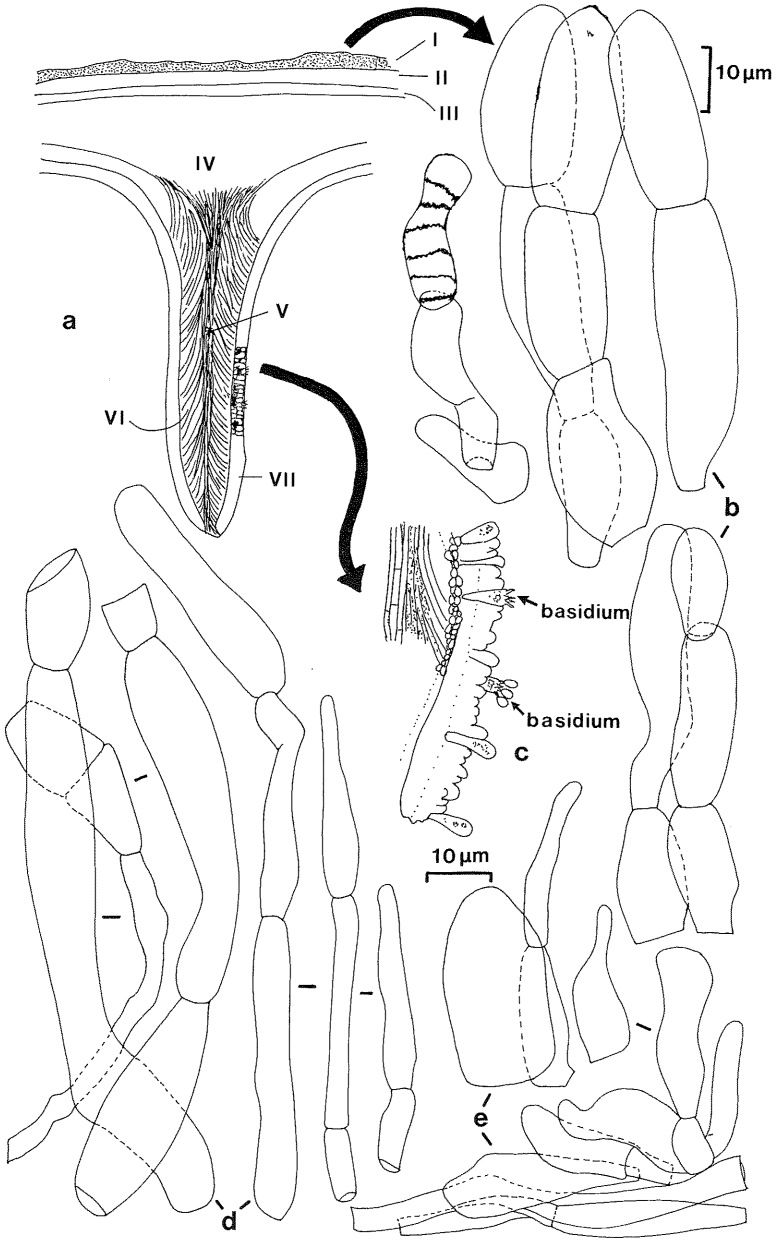


FIG. 8. *Armillaria ostoyae*. a, section of gill with attached pileal tissue under low power, I suprapellis, II mediopellis, III subpellis, IV context, V mediostratum, VI divergent hymenophoral trama, VII hymenium; b, cells in I; c, hymenium in VII; d, elements of veil; e, elements from veil-margin. All from *Watling* 11509.

age, upper-surface with blackish brown scales on margin pointing outwards and tipping small white floccules, resembling a spiked wheel, and leaving white cortinate wisps of veil at pileus-margin. *Gills* close, adnate with distinct tooth or almost subdecurrent from gill-striae composed of punctae extending down to ring, white at first then with distinct tinge of pinkish straw-colour, or yellowish buff, pinkish or even brownish hue becoming most intense with age, bruising clay-pink. *Flesh* white in stipe at first then pale pinkish buff, flushed fuliginous or buff in stipe base, and dark cinnamon in stipe cortex, white to pale pinkish buff or cinnamon pinkish in pileus with dark line over gills; *taste* mild at first but after considerable mastication slowly and slightly soapy which lingers for a long time; *smell* of earthballs (*Scleroderma*).

Basidiospores D, crême moyen (Romagnesi) in mass, inamyloid, ellipsoid to broadly ellipsoid with prominent hilar appendage, 6·5–$10 \times 4{\cdot}4$–5·5μm, slightly hyaline or yellowish honey-colour in alkali particularly after storage, weakly cyanophilic, moderately thick-walled, smooth or very slightly verruculose or asperulate (Fig. 8c). *Basidia* 4-spored, rarely 2-spored, usually hyaline, rarely becoming thick-walled (crassobasidia) but then yellowish, without basal clamp-connection, 38–$41 \times 7{\cdot}5$–8·5μm, sterigmata stout, straight, $<3{\cdot}3\mu$m long (Fig. 8e). *Cheilocystidia* present, quite conspicuous in some mounts, very variable, either ampulliform to lageniform (22–50μm long) with neck 7–11μm long and head 2·75–4μm wide or clavate (Fig. 8d); *pleurocystidia* absent, or if present reduced to thin-walled, poorly differentiated cells rarely visible above the level of basidia and possibly representing undifferentiated basidioles; all cystidia lacking basal clamp-connections. *Pileipellis* consisting of an irregular suprapellis composed of groups of fulvous or cinnamon-coloured, sausage-shaped cells $\pm$ spirally pigmented, 22·5–$42.5 \times 8{\cdot}5$–12·5μm, loosely or strongly adhering together to form subparallel ascendant clusters of hyphae forming 'scales', and intermixed with smooth, hyaline, narrower hyphae (Fig. 8b); *suprapellis* disrupting with age, constituent hyphae ascendant becoming repent to form a rather irregular layer seated on a mediopellis of parallel to subparallel hyphae which finally becomes, in places, the outermost layer (cutis); *subpellis* more compacted, hyaline. *Stipitipellis* of parallel hyphae (7.5–10μm) overlain by irregularly swollen and entangled hyaline hyphae $<12\mu$m broad and in places additionally overlain by dark brown swollen chains of cells resembling those of the pileipellis. *Velar material* of ring composed of silvery, relatively thin-walled, filamentous, flexuous to cylindric, intertwined, floccose hyaline, generally smooth hyphae 2·5–4μm broad, often strongly adhering in plates and then elements becoming shortened, passing into richly coloured, broader ($<8\mu$m), shortened ($<10\mu$m) cells loosening towards the apices of the hyphae to resemble chains of orange-brown sausages with penultimate and terminal cells towards the ring-margin often tapering to become 'torpedo-shaped' and similar to those in suprapellis. Lower surface of ring composed of hyphae arranged in alternate bands of hyaline and of dark brown hyphae, the latter with terminal cells much the same as those in the peripheral areas of the ring and suprapellis: composed of a mixture of highly branched, hyaline hyphae $15–27{\cdot}5 \times 3{\cdot}3$–5$\mu$m with smooth or slightly irregular wall within

and constricted at the septa, and red-brown to tawny or orange-brown, thick to thin-walled, smooth or very slightly irregular hyphae 9–35 × 4·5–8μm constricted at septa and disarticulating, seated on hyaline, cylindric, thin-walled, hyphae 2·5–3μm broad adhering in a basal layer with parallel arrangement. *Pileus-trama* inamyloid, monomitic, of floccose, hyaline hyphae lacking clamp-connections. *Hymenophoral trama* bilateral, at first with lateral trama diverging from slightly gelatinized mediostratum and terminating in a 'cellular' compact subhymenium (Fig. 8a, c).

Habitat: on standing or fallen living and dead trunks of both coniferous and deciduous trees.

Collections examined: England, Cheshire, Lyme Park near Stockport (a public recreation area with a wide range of native and exotic trees), on fallen *Pinus sylvestris,* 4 x 1980, *Watling* 13747 (E); Lancashire, Gaitbarrows National Nature Reserve (a protected woodland with mixed frondose trees and *Taxus baccata*), on fallen tree, 20 x 1978, legit D. & L. Livermore (*Liv.* 38/78), *Watling* 13152 (E); Yorkshire, Hardcastle Crags, Hebden Bridge, on dead *Ulmus* (due to Dutch elm disease), 29 ix 1984, legit M. Storey, *Watling* 18059 (E); Yorkshire, Foul Scout Wood, Hardcastle Crags, Hebden Bridge, on *Fraxinus,* 29 ix 1984, legit M. Storey, *Watling* 18074 (E); Yorkshire, Eccleshall Wood, Sheffield, on *Rubus idaeus*, 19 x 1975, *Watling* 11489 (E). Scotland, Dunbartonshire, Inchlonaig, Loch Lomond (a semi-natural woodland on an island with mixed frondose trees and very old *Taxus*), on *Ilex,* 13 x 1975, *Watling* 11509 (E); ibid., on *Taxus,* 13 x 1975, *Watling* 11495 (E); ibid., on *Sorbus aucuparia,* 13 x 1975, *Watling* 11488 (E); Ayrshire, Torr Knowe Wood, near Straiton, crop of pure Sitka spruce planted in 1971 showing large *Armillaria* killing, on *Picea sitchensis,* 15 vi 1978, legit S. C. Gregory (G2 NRS); ibid., legit S. C. Gregory (G2R NRS)—a further collection (BQIF) was made within 10m, $4\frac{1}{2}$ years later and confirmed in mating tests as *A. ostoyae* (Gregory, pers. comm.). Perthshire, Comrie, isolated from rhizomorphs on *Pinus* sp. (no voucher material kept).

The collection above from *Pinus sylvestris* (*Watling* 13747) had all the characters delimited by Romagnesi (1970, 1973) for *A. obscura,* lacking all pinkish hues normally associated with *A. ostoyae,* and only possessing small dark brown scales both on the pileus and ring margin. The culture, however, was compatible with tester strains of *A. ostoyae.*

Korhonen (in litt. 1981) wrote 'results were very clear. The specimen identified as *A. obscura* is clearly interfertile with the representatives of *A. ostoyae* Romagn. (i.e. 'sp. C'). The real existence of *A. obscura* has thus not yet been shown'. Marxmüller (1982) showed that her isolates of *A. obscura* were also compatible with *A. ostoyae.*

Armillaria ostoyae is frequently found in the forest environment where basidiomes have been found fruiting on a range of hosts especially shrubby plants (e.g. *Watling* 11488 and *Watling* 11489). Generally the species is found on arborescent taxa and is often isolated from diseased forest trees (Rishbeth, 1985; Gregory, pers. comm.).

Of all the species in the *A. mellea* complex, *A. ostoyae* is the taxon which most commonly produces primordia and even mature basidiomes in pure culture. In common with other European taxa the development

would appear to be both metavelangiocarpic and stipitocarpic. The velar development on the pileus produces erect columns of dark brown cells which form the characteristic scales, a feature echoed at the margin of the annulus and lower part of the stipe. The tissue protecting the maturing gills is relatively well-developed and at maturity splits to form a white membranous ring girdling the stipe. This structure with its prominent dark brown cog-like margin characterizes this agaric in the field and absence of the latter is a strong argument for rejecting the use of *Ag. obscurus* Schaeffer for this species.

Transmission electron microscope studies show that the outer surface of all the basidiospores are irregular, a feature, however, only seen under the light microscope in certain collections, or spores within a single collection.

Additional Species

Armillaria borealis

A. borealis Marxmüller & Korhonen has been located in at least seven localities in Scotland on both native and introduced trees (Gregory & Watling, 1985).

Material agreeing in all macro- and microscopic characters has since been located at Struan Wood near Calvine, Perthshire (on *Betula,* 22 ix 1983, *A. Strid* s.n., S) and Dalreiach near Enochdhu, Perthshire (on *Betula*, 29 vii 1985, *Watling* 18695, E), (Watling, 1984).

The development of the basidiomata has been interpreted from mounts prepared from fresh material from both Struan and Dalreiach, where in both instances it forms tight clusters of basidiomata often above shoulder height and emerging from old wounds where former limbs had fallen. In these studies *A. borealis* would appear to agree in all respects with *A. ostoyae* except that the pileal and marginal scales are not as prominent nor the annulus as persistent.

The basidiospores of *A. borealis* are slightly irregular in outline under the transmission electron microscope although as in *A. ostoyae* it is difficult to pick this character up in light microscope mounts.

Armillaria mellea

A. mellea (Vahl: Fr.) Kummer has been discussed in full and descriptions of material from both England and Denmark have been given (Watling, Kile & Gregory, 1982—when a neotype was designated).

Although *A. mellea* would appear to be generally more common southwards in Great Britain good collections have been made on *Quercus* in Yorkshire (*Watling* 16459), Midlothian (*Watling* 14187) and Ardtornish, Morven, Argyll (*Watling* 19495). Typical material has been seen at Blackspout Wood, Pitlochry, Perthshire (*Watling* 17451, 17456 & 17465), although cultural studies have not been conducted. These Scottish localities are ancient oak woods and the Pitlochry area is noted for its southern elements, e.g. *Porphyrellus porphyrosporus* (Fr. & Hök) Gilbert (=*P. pseudoscaber* (Secr.) Sing.), *Heteroporus biennis* (Fr.) Laz. and *Lycoperdon echinatum* Pers.

A. mellea is highly pathogenic in laboratory experiments (Rishbeth, 1982, 1985) and especially in the south of England it characteristically has

a wide host-range. It has in fact been isolated from hosts other than *Quercus* in Scotland. One interesting series of basidiomata came to light in a garden in Edinburgh—interesting because the basidiomata were fruiting on a range of hosts (see *Watling* 11401–11407 below) and they lacked the characteristic yellow margin to the annulus and ochraceous colours to the pileus. As has been found with *A. lutea* and *A. luteobubalina* (Kile & Watling, 1983) greyed forms which are completely interfertile with the classic forms are not infrequent.

These collections also exhibit the range of variability found in the Australian *A. luteobubalina* with thicker set basidiomata when only a few are found in a cluster, and indeed the characteristic cylindric stipe under such circumstances may become quite stout: *A. luteobubalina* and *A. mellea* are very close; the development has been confirmed as being metavelangiocarpic in both. *A. mellea* is characterized by a long, cylindric stipe elongating, during a long stipitocarpic stage, surmounted by an apical, usually yellow marginal annulus.

Both transmission and scanning electron microscope studies have shown that the outer wall of the basidiospores of *A. mellea* is either smooth or only slightly irregular in contrast to those of *A. lutea*.

Collections examined: England: Warwickshire, Chesterton Park, on old (?*Fagus*) stump, 29 ix 1979, *Watling* 13386 (E); ibid., on old stump, 29 ix 1979, *Watling* 13387 (E, as *A. nigritula* Orton); ibid., on old stump, 3 x 1982, legit B. Brand, *Watling* 16528 (E). Lancashire, Lyme Park, on *Fagus,* 4 x 1980, *Watling* 13745, 13746 (E). Yorkshire, Saw Wood near Leeds, on *Quercus,* 19 ix 1982, *Watling* 16459 (E). Scotland: Midlothian, Dalkeith, on *Quercus,* 19 ix 1981, *Watling* 14187 (E); Edinburgh, Brunstane House, on *Malus,* 24 x 1975, legit S. Higgnett, *Watling* 11406 (E); ibid., on stump, 24 x 1975, legit S. Higgnett, *Watling* 11403, 11405 (E); ibid., on *Escallonia,* 24 x 1975, legit S. Higgnett, *Watling* 11401 (E); ibid., on *Helianthus tuberosus* (Artichoke), 24 x 1975, legit S. Higgnett, *Watling* 11404 (E); ibid., on *Symphoricarpus,* 24 x 1975, legit S. Higgnett, *Watling* 11407 (E). Ayrshire, House Cellars Wood, Blairquhan Estate, near Straiton, from ground near *Fagus sylvatica* with *Larix* × *eurolepis* and *Quercus* stumps nearby, 28 ix 1982, legit S. C. Gregory (BQSF). Argyll, Ardtornish, Morven, Loch Anenas, on *Quercus,* 27 viii 1986, *Watling* 19495 (E). Perthshire, Blackspout Wood, Pitlochry, on *Quercus,* 9 ix 1984, *Watling* 17451, 17456, 17465 (E).

Armillaria cepistipes

This is Korhonen's 'sp. B' (Korhonen, 1978), and the more commonly found form is separated by Romagnesi & Marxmüller (1983) as forma *pseudobulbosa* (as *A. pseudobulbosa* (Romagnesi & Marxmüller) Arnolds & Termorshuizen, see Roll-Hansen, 1986). It is very close to *A. lutea* (syn. *A. bulbosa* auct.; see above) in external morphology (hence the epithet) and difficult to identify on classical characters in the field. Although it has been identified from cultures isolated from plant-tissue in Scotland (S. C. Gregory, pers. comm.), it has not been recognized as such in the field. Only old basidiomes have been found and never the whole range of specimens necessary for a full description and therefore no description of

British material is made at present. Rishbeth (1985) does not deal with this species in his study of resources and hosts in *Armillaria* in southern England. Its distribution in the British Isles is at present unknown and the taxon is under further investigation.

A Cautionary Note

It would be folly to reintroduce any further old names in the future for any armillarioid agaric when their descriptions lack adequate information for modern delimitation.

If a good plate can be used which depicts all the salient characters of a particular agaric taxon, then a case may be argued, but critical data is required for *Armillaria* studies to develop further. Species of *Armillaria* are notoriously difficult to identify in the field on macroscopic characters alone, and little better when microscopic data is available. It has been experienced that no better than 65% of field collections can be identified on macroscopic characters alone. Of the 35% remaining, 20% are incorrectly named prior to cultural characterization. The typical material is relatively easy to deal with but there are many collections which do not fall into this category. Thus, unfortunately, even when dried material is available in the classical herbaria a definite identification cannot be made, unless there is an excellent colour illustration in manuscript or published form supporting the collection. Now there is the opportunity, new species of *Armillaria* should always be accompanied by cultural data with a culture deposited in a national collection.

The significance of the basidiospores in separating species of *Armillaria* appears to be of limited value. The first spores shed from *A. lutea Watling* 13387 immediately on collection ($7{\cdot}2–8{\cdot}9 \times 4{\cdot}4–5{\cdot}6\mu m$) are similar in dimension to those of *A. mellea,* one hour and two hours after collection ($7{\cdot}2–8{\cdot}9(–9{\cdot}5) \times 5{\cdot}6–6{\cdot}7\mu m$: $7{\cdot}2–8{\cdot}9 \times 5{\cdot}6–6{\cdot}7\mu m$), and similar to those shed after 24 hours ($7{\cdot}2–8{\cdot}9 \times 4{\cdot}4–6{\cdot}1\mu m$). It would appear in this case that the spore dimensions are very constant. There is some evidence, however, that this may not be so in other taxa (Kile & Watling, 1983) and throws some doubt onto the use of small differences in spore sizes to distinguish taxa in *Armillaria.*

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