OBSERVATIONS ON THE BOLBITIACEAE 12:
The affinities of two anomalous species

ROY WATLING

ABSTRACT. A reassessment of two anomalous North American agarics has made necessary the following new combinations: *Conocybe michiganense* (A. H. Smith) Watling; *Agrocybe leechii* (A. H. Smith) Watling; and sect. *Conocybella* (Singer) Watling of *Conocybe* subgenus *Conocybe*.

INTRODUCTION

Since the starting point publication of Fries (1821), the colour of the spore-print has greatly influenced the decisions of mycologists classifying agarics. The literature contains many taxa which demand immediate attention in order to ascertain their true affinities but many of these fungi were described in the era before anatomical details were considered essential. A few anomalous members scattered in various genera have been described more recently with appropriate microscopic data, and two with rather dark spore-prints, now assignable to the family Bolbitiaceae, are the subject of this communication.

1. PSATHYRELLA MICHIGANENSE

In 1951 Singer erected *Psathyrella* subgenus *Conocybella* to accommodate *P. michiganense* A. H. Smith. It was erected as a logical continuation of subgenus *Psathyrella* with its members differing only in the characters of the cheilocystidia; the subgeneric name was used to emphasise the similarity with the lecythiform cheilocystidia found in *Conocybe*. Smith (1972) has stated "if an origin of the Coprinaceae from the Bolbitiaceae is accepted, then this group (which includes only the type species) is possibly a primitive *Psathyrella*. No matter how one visualises the phylogeny of the agarics the type species is certainly a good intermediate between the two families".

I have had the opportunity to examine all the material available to Smith when he drew up his monograph (1972) of North American species of *Psathyrella* and found, as Smith has indicated, that the basidiospores of *P. michiganense* are not now as dark as was implied by the original description. Smith says "in fact they now appear to be 'off-colour' *Conocybe* spores". Smith characterised *P. michiganense* with its small, fuscous basidiospores, ventricose cheilocystidia with an apical button, pubescent pileus and stipe, and slender habit.

The cheilocystidia of *P. michiganense* in no way differ from those of the *Conocybe tenera* group, having a ventricose mid-portion with an abrupt narrow neck terminating in a subglobose head (or capitellum), i.e. they are lecythiform. Indeed the pileipellis of *P. michiganense* is more in keeping with the genus *Conocybe* than it is with the genus *Psathyrella*. The pileipellis is a hymeniderm, composed of a palisade of inflated and stalked (pedicellate) cells, slightly thickened towards their bases. These cells are arranged in an

orderly fashion and are not stacked in a brick-like pattern as is found in the pileipellis of many species of *Psathyrella*. In addition to this, slender, thin-walled hyaline hyphae project beyond the undulating layer formed by these swollen cells. It is these hyphae which give to the fresh pilei the minutely pubescent nature described by Smith in his original notes. They originate between the swollen cells in the subpellis in much the same way as has been described by Watling (1964, 1975) for the hairs, or true pilocystidia, of members of the *Conocybe pubescens* group.

The stipe is also described by Smith in his original notes as being densely pubescent. An examination of the stipes of the type and subsequent collections shows that the pubescence is composed of numerous groups of caulocystidia. These caulocystidia are not lecythiform; they are ventricose, lageniform etc. and intermixed with numerous extremely long, thin-walled, hyaline cells similar to the pilocystidia. To my knowledge, such a pattern of both differentiated caulocystidia and long flexuous hairs does not exist in *Psathyrella* but it does in *Conocybe* sect. *Pilosellae*. Indeed in this same group of *Conocybe*, dermatocystidia in the pileipellis are frequent, particularly if the fruit-bodies are grown or maintained in an atmosphere of high humidity.

The basidia of *P. michiganense* are quite short, as would accord with a placement in the Bolbitiaceae, and there are no pleurocystidia. Pleurocystidia are rare or unknown in *Conocybe* and *Bolbitius*.

The structure of the basidiospores in all ways agrees with the placement of *P. michiganense* in either the Bolbitiaceae or Coprinaceae. The spores are smooth, truncate because of a hyaline, central apical germ-pore, broadly elliptical to slightly flattened in one plane in side-view, and in some slightly angled. The basidiospores are dull fuscous when mounted in water and silicone oil but in aqueous solutions of 0·88 ammonia, and of potassium hydroxide they take on a more amber coloration i.e. darkening. This darkening is a characteristic of all members of the Bolbitiaceae so far examined. Smith (1941) records the fresh spores as very dull fuscous brown under the microscope but this coloration has somewhat faded over the last thirty or so years. Equally the pigment bringing about the blackish reaction with potash originally noted has been apparently modified. The presence of such a pigment is unusual; although changes in spore-print colour do occur, few if any observations have been made on changes in wall-pigment. The dark pigment can be dispersed by the application of concentrated sulphuric acid but it then leaves clear golden yellow spores indistinguishable from most species of *Conocybe*.

The presence in *Conocybe* of a species with a fuscous spore-print is not altogether unexpected since one as yet unnamed *Bolbitius* from the Himalayas has a similar anomalous spore-print colour, and Singer (1962) mentions the existence of a second species perhaps close to *B. nobilis* Peck in Virginia, North America.

The pileus-trama of *P. michiganense* is composed of irregularly interwoven enlarged cells. The hymenophoral trama in *Psathyrella* is of interwoven to somewhat subparallel hyphae which in older fruit-bodies may inflate considerably. Typically the subhymenium is pseudo-parenchymatous. In the Bolbitiaceae although a regular gill-trama is present it is of a more differentiated pattern with filamentous cells reduced to a thin bundle confined to the centre of the gill and the cells on either side so inflated as to almost obliterate

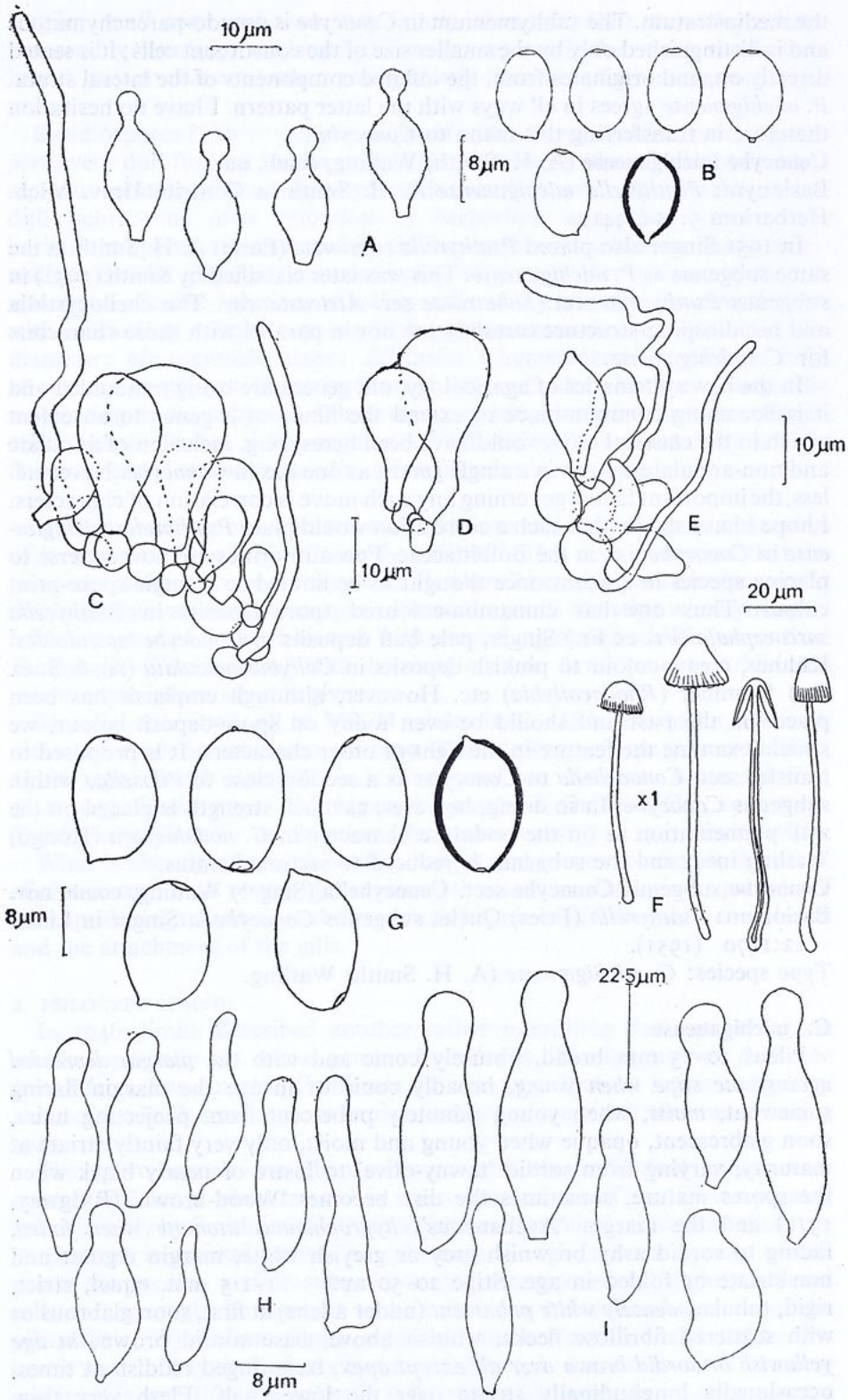

FIG. 1. A–F, *Conocybe michiganense*: A, cheilocystidia; B, basidiospores; C, hymeniderm; D, individual cells from hymeniderm; E, caulocystidia; F, habit sketch; G–I, *Agrocybe leechii*; G, basidiospores; H, cheilocystidia; I, pleurocystidia.

the mediostratum. The subhymenium in *Conocybe* is pseudo-parenchymatous and is distinguished only by the smaller size of the constituent cells; it is seated directly on, and originates from, the inflated components of the lateral strata. *P. michiganense* agrees in all ways with the latter pattern. I have no hesitation therefore in transferring this taxon to *Conocybe*:

Conocybe michiganense (A. H. Smith) Watling, **comb. nov.**

Basionym: *Psathyrella michiganense* A. H. Smith in Contrib. Univ. Mich. Herbarium 5:35 (1941).

In 1951 Singer also placed *Psathyrella roystonae* (Earle) A. H. Smith in the same subgenus as *P. michiganense*. This was later classified by Smith (1972) in subgenus *Psathyrella* sect. *Subatratae* ser. *Atricastaneae*. The cheilocystidia and basidiospore-structure certainly are not in parallel with those characters for *C. michiganense*.

In the new systematics of agaricology, old genera are being remoulded and it is becoming common-place to extend the limits of a genus to an extent which in the classical days would have been heresy, e.g. inclusion of annulate and non-annulate agarics in a single genus, as one has in *Conocybe*. Nevertheless, the important factor governing any such move is correlation of characters. I hope I have shown that such a correlation would place *Psathyrella michiganense* in *Conocybe*, i.e. in the Bolbitiaceae. Few authorities are now adverse to placing species in a genus once thought to be limited to a single spore-print colour. Thus one has cinnamon-coloured spore-deposits in *Psathyrella sarcocephala* (Fr. ex Fr.) Singer, pale buff deposits in *Conocybe* '*spiculoides*' Kühner, cream-colour to pinkish deposits in *Collybia maculata* (A. & S. ex Fr.) Kummer (*Rhodocollybia*) etc. However, although emphasis has been placed in the past and should be even today on spore-deposit colour, we should examine the feature in the light of other characters. It is proposed to transfer sect. *Conocybella* to *Conocybe* as a section close to *Pilosellae* within subgenus *Conocybe*. In so doing, however, as much strength is placed on the wall pigmentation as on the nodulose character in *C. nodulospora* (Hongo) Watling ined. and the subgenus is reduced to sectional status.

Conocybe subgenus **Conocybe** sect. **Conocybella** (Singer) Watling, **comb. nov.**

Basionym: *Psathyrella* (Fries) Quélet subgenus *Conocybella* Singer in Lilloa 22:1470 (1951).

Type species: *C. michiganense* (A. H. Smith) Watling.

C. michiganense

Pileus 10–25 mm broad, obtusely conic and with the *margin depressed against the stipe when young*, broadly conic or in age the margin flaring somewhat, *moist*, when young minutely pubescent from projecting hairs, soon glabrescent, opaque when young and moist, only very faintly striate at maturity, varying from sordid 'tawny-olive' to bistre or nearly black when the spores mature, sometimes the disc becomes 'Wood-brown' (Ridgway, 1912) and the margin 'Avellaneous', *hygrophanous atomate when faded*, fading to sordid ashy brownish grey or greyish white, margin regular and non-striate or folded in age. Stipe 20–50 mm × 1–1·5 mm, equal, strict, rigid, tubular, *densely white pubescent* (under a lens) at first, soon glabrous or with scattered fibrillose flecks, whitish above, base sordid brown, *in age yellowish or sordid brown over all except apex*, base tinged reddish at times, occasionally longitudinally striate over the lower half. Flesh very thin,

fragile; *smell* none and *taste* very faintly of radish. *Gills ascending adnate*, not readily seceding, moderately close (23–27 reach the stipe), moderately broad, pale avellaneous when young slowly becoming fuscous brown, edges even.

Basidiospores 8–10 × 5–6 μm, *ellipsoid* with *obvious*, *hyaline*, *central germpore*, very dull fuscous brown under the microscope when fresh, blackish in aqueous solution of potassium hydroxide (Smith, 1941), pallid snuff-brown to dull ochraceous after retention in herbarium and snuff-brown when herbarium spores are mounted in similar hydroxide solutions, fairly thick-walled. Basidia 4-spored, clavate, squat, 18·5–22 × 8·5–10 μm, hyaline in water and alkaline solutions. *Cheilocystidia* 18–25 × 10–15 μm, lecythiform with a swollen venter, 2–3 μm high neck surmounted by head 3–4 μm diameter; *pleurocystidia* absent. *Pileipellis* a hymeniderm of pyriform cells, 18–50 × 10–30 μm high, intermixed with slender, hyaline pilocystidia originating in the subpellis. Pileus trama of irregularly interwoven enlarged cells. *Hymenophoral trama* regular, of inflated cells separated by a thin, floccose central strand reduced to a few filamentous hyphae.

Smith's description is repeated with additions and the important characters of a member of the genus *Conocybe* italicised. This does not mean that the same characters cannot be found in *Psathyrella* except perhaps the careful original observation that 'margin adpressed against the stipe when young' is a feature more of the Bolbitiaceae with paravelangiocarpic development than *Psathyrella* (Coprinaceae) with bivelangiocarpic development. Additional microscopic information is given.

Material examined, all in MICH; slides in E. USA: Michigan, Milford, old wood road, on sawdust, 9 vii 1939, *Smith* 9587 (paratype); same locality, 15 ix 1939, *Smith* 10920 (holo.); Tennessee, on sawdust, Anderson Co., 31 x 1943, *Hesler* 15918, Michigan, in grassland, Oakland Co., 19 x 1950, *Smith* 36255. Canada: on chip dust, Petawawa forest, 3 ix 1947, *Smith* 26469.

What is also significant about this fungus and its new placing is the detail of the construction of the hymeniderm, the familiar darkening upwards of the stipe during maturation, the persistently conic cap (*Conocybe*—cone-head) and the attachment of the gills.

2. PSILOCYBE LEECHII

In 1946, Smith described another rather interesting dark-spored agaric which apparently cut across generic boundaries. The fungus was *Psilocybe leechii* from Los Angeles, California. It was gregarious on lawns and grassy areas of the UCLA campus; several collections of the taxon were made during 1945.

The spore-deposit was 'Benzo-brown' and the individual spores were ochraceous tawny when revived in aqueous solutions of potash. As pointed out originally by Smith (1946), this species has a 'cellular' cuticle and therefore its position is anomalous in *Psilocybe* even though in some species of this genus the medio- and/or subpellis may be composed of slightly inflated cells and so might be thought to be cellular in hasty hand-sections of the pileipellis cf. *Hypholoma*. Smith reported that the "cuticle" exhibited by this taxon was "not typical of any species of *Agrocybe* known to me". In many species it is true that the palisade cells of the hymeniderm in *Agrocybe* are

relatively short and inflated instead of narrowly clavate and with thick-walled pedicels. Basal thickening of the hymeniderm elements is in fact found in several members of the Bolbitiaceae both in *Conocybe* and *Agrocybe*, especially those with a more persistent fruit-body and/or where the fruit-body takes some time to develop, e.g. *Agrocybe dura*, in contrast to *Conocybe lactea*, *Bolbitius vitellinus* etc.

The gills of type material of *P. leechii* are at present dark snuff-brown in colour and this agrees very favourably with the gills of several species of *Agrocybe* close to and including *A. semiorbicularis*, indeed even those housed in the same herbarium collection as *P. leechii* (MICH), and elsewhere (E). The basidiospores are rather thick-walled which might account for the darker spore-deposit. I have matched Leech's spore-deposit with a Ridgway colour chart and some 30 years later it is in good agreement with that of an *Agrocybe*. Watling (1964) has shown that spore-deposits obtained from *Agrocybe* spp. where *Collembola* are active are darker than those in areas even of the same fruit-body where the *Collembola* are not feeding. Examination in silicone oil of these dark coloured basidiospores shows them to be concavo-convex whereas the other spores are plano-convex or bi-convex; the contents have been sucked out of the spores and the 'shells' are bound together in small groups by invertebrate gum. Thus it is easy to move from one hue in the browns to another in a single genus—even a single specimen. Unlike the treatment of *C. michiganense* I do not propose to recognise a separate section for this Californian taxon. The following treatment is therefore proposed:

Agrocybe leechii (A. H. Smith apud Smith & Hesler) Watling, **comb. nov.**

This fungus should be placed in *Agrocybe* subgenus *Agrocybe* sect. *Pediadeae* (Fries) Singer.

Basionym: *Psilocybe leechii* A. H. Smith apud Smith & Hesler in Journ. Elisha Mitchell Scientif. Soc. 62(2):196 (1946).

Pileus 20–40(–50) mm, convex to slightly umbonate with an inrolled margin, becoming hemispheric to slightly umbonate, glabrous or with very slight remnants of a white rudimentary veil along the margin when young, golden brown, ochraceous tawny overall and gradually becoming pale tan, lubricous when fresh but soon dry, somewhat fleshy. *Stipe* 30–70 × 2·5–5·5 mm, slender, equal or nearly so, pallid alutaceous but gradually darkening to greyish but when dry becoming alutaceous again, pruinose overall, or with scattered fibrils over the lower portion from the veil, stuffed*, cartilaginous. *Gills* rounded, adnate to adnexed (slightly attached to the stipe), broad, close with two tiers of lamellulae, dark tan to pallid becoming nearly cinnamon drab. *Flesh* thick, pallid; *odour* and *taste* not recorded.

Basidiospores near 'Benzo-brown' in mass, 13–16 × 9–11 μm smooth, thick-walled, hyaline germ-pore small and slightly eccentric as seen in side-view, ochraceous tawny when revived in aqueous ammoniacal or potassium hydroxide solutions. Basidia 2-spored, hyaline in alkali solutions, 34–40 × 9–10 μm. *Pleurocystidia* rare to scattered, 35–55 × 9–14 μm, thin-walled, ventricose with broadly rounded to capitate apices some becoming subcylindric to utriform, hyaline in potassium hydroxide solutions. *Cheilocystidia* similar to pleurocystidia but smaller, fusoid-ventricose and variable some only

* Leech's field-notes in fact read 'Better description of this would be a separate narrow tube within stipe, i.e. characteristic of stipe of *A. temulenta* (Cke.) Singer.

20–25 × 5–8 μm. *Hymenophoral trama* of slightly interwoven hyphae, hyaline in aqueous alkaline solutions, hyaline towards the subhymenium. *Pileipellis* a hymeniderm of narrowly clavate cells 30–40 × 4–7·5 μm, pale yellowish, tawny towards their base, with thickened walls at base, upper thin-walled portion soon collapsing. *Pileus trama* of bright tawny brown hyphae below pileipellis, with encrusted walls. *Clamp-connections* present.

A number of characters other than the structure of the basidiospore and 'cellular' cuticle place this in the Bolbitiaceae and not *Psilocybe* (Strophariaceae), the latter as redefined by Orton (1969); one character particularly is the presence of pleurocystidia. Indeed, the pleurocystidia are exactly as those found in the *A. semiorbicularis* group. Re-reading Leech's notes one finds he thought the material was *Naucoria semiorbicularis* and mentions 'rust spores'. Could not the 'change' have taken place en route from California to Michigan? If the spores are mounted in silicone oil they are found in small packs similar to those found after invertebrate activity on the deposited spore-print; there is every possibility that active feeding could have taken place in the protective environment of the mail. What is most significant is, I believe, the presence of an eccentric germ-pore. I have now had the opportunity to examine hundreds of specimens of the genus *Agrocybe* and this is the first time this character has appeared. Smith noted it but did not emphasise its uniqueness, even in *Psilocybe*. However, possession of an eccentric germ-pore only extends this character from the numerous species of *Coprinus*, *Psathyrella* (Watling & Jurand, 1971), *Conocybe* (Watling 1964) now to *Agrocybe*.

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