OBSERVATIONS ON THE BOLBITIACEAE

2. A CONSPECTUS OF THE FAMILY*

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The author gives a recapitulation of the genera, subgenera and sections of the *Bolbitiaceae*. He is inclined to recognise three genera which are fully described; the genera he is not prepared to uphold are discussed. The synonymy of the genera and infrageneric taxa is listed. The treatment of each genus does not go further than the delimitation of subgenera and sections, and citation of type species. A key to the subgenera and sections is given. An introductory chapter contains some general remarks on the family. Keys to the genera of brown-spored agarics in the British Isles and in the World are given. Relationships of bolbitiaceous genera with other agaric groups are carefully considered.

INTRODUCTION

The family *Bolbitiaceae* forms a well-defined group which has long been neglected by both formal and experimental taxonomists. In fact, from a review of the literature, not only have very few of the members of the family been experimentally investigated but few have been obtained in pure culture.

Although the constituent genera of the family have been examined by classical taxonomic methods of agaricology, the family has never been critically studied as a unit, until comparatively recently. Even with descriptions scattered throughout the literature of the main genera, at least some in considerable detail, the information has never been brought together in monographic form.

The *Bolbitiaceae*, as currently accepted, was first recognised in the literature as a distinct group of fungi by Heim (1931), although Fayod (1889) foresaw its existence when he defined his tribe "Naucoriés". Subsequently, Singer (1936) gave it subfamily rank; yet it was not until twelve years later that he erected the family name now used. Singer (1948) considered the forms he included under this name as a very natural group of agarics; if this be the case it is unlike some of the other families currently accepted in the Agaricales. The diagnostic characters on which this natural group was based were the smooth, brown (rust—hazel-brown) basidiospores which have usually a thickened wall and a prominent germ-pore, the hymeniform epicutis, and the presence of specialised cells on the gill-margin. Singer (1951) amplified these concepts in his impressive work "The Agaricales in Modern Taxonomy". The family name he derived from that of the genus he selected as type, *Bolbitius*, and he included in the family seven genera. There is little doubt that Singer's ideas on the *Bolbitiaceae*, as in many other groups of the agarics, were moulded around the original principles of Fayod (1889). Singer extended to all the major agaric groups, including the *Bolbitiaceae*, the latter's work on the application of anatomy and development to an understanding of the taxonomy and affinities of this group of higher fungi.

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* Some of the results in this paper are taken from a thesis accepted for the degree of Ph.D. in the University of Edinburgh.

Indeed Fayod originally not only described the two most prominent genera in the family, *Agrocybe*, with hazel-brown spore-print, and *Conocybe*, with rust-brown spore-print, but also the genus *Pholiotina*. There is much discussion about the latter genus as to its placing within the family and whether it is in fact distinct enough to merit generic status.

In compilation of notes and keys on the genus *Agrocybe*, Singer (1936) again was an important forerunner. Of the other genera of the family *Bolbitiaceae* Kühner (1935) produced a beautiful annotated account "Le genre Galera" based primarily on fresh collections. Kühner's treatment of the old Friesian tribe *Galera* laid down the foundation of many modern studies on the *Bolbitiaceae*, both directly and indirectly. He recognised that the genus *Galera*, a generic combination made by Kummer embracing Fries's original tribe *Galera*, was in fact polygeneric and separated out the West European members into the two important components *Conocybe* and *Galerina*. Although members of the latter genus had always stood in earlier works beside true members of the family *Bolbitiaceae*, Fayod, Atkinson (1918) and Kühner found them to be in fact only superficially similar. The variation, however, in the genus *Galera* was well known to Fries himself, who recognised (1838) two major groups and although he placed them both in a single tribe and, later, subgenus of *Agaricus* he distributed one, i.e. *Conocybe*, in the section *Conocephalae* and the other, i.e. *Galerina*, in the section *Bryogenae*.

Kühner's and Singer's papers in conjunction with the introductory chapter on the brown-spored agarics in Heim's "Le genre Inocybe" are the starting points in the modern analysis of the *Bolbitiaceae*. Heim (1931) in the same publication described a new genus for the family, i.e. *Tubariopsis*, and a new subgenus of *Conocybe*, i.e. *Cyttarophyllum*, both from Madagascar. He recognised their affinities to the temperate species of *Conocybe* and *Bolbitius* and in a key to the brown-spored groups refers to them all as the "Série des Pholiotes; Groupe des Bolbitius". Kühner arranged the agarics he placed in *Conocybe* into 2 subgenera, "*Eu. Conocybe* and *Pholiotina*", the former being split into two sections. Of the sections of his *Eu. Conocybe*, *Capitatae* and *Piliferae*, the former was split further into three subsections. Singer (1947, 1951, 1962) in his later studies, although raising many of Kühner's subsections to higher rank, does in fact retain the major groupings first established by this meticulously careful French mycologist.

Since Kühner's publication and Singer's earliest systematic work on the genus *Agrocybe* many new species have been described which are now attributable to the family. However, there has been no recent revision of the family and both the taxonomy and the nomenclature, especially the latter, are sliding into chaos (see Orton, 1960). This is especially the case since the discovery and examination of Central Asiatic and of South and Central American bolbitiaceous agarics.

Much attention has been paid to the gastromycetoid members of the family (Heim 1950, Singer 1951, 1953 and 1962, etc.) especially after Singer discussed as early as 1936 the position of *Raddetes* Karst. and Heim described *Conocybe* subgen. *Cyttarophyllum*. Herbarium material including type specimens have been examined and in many ways it is difficult to decide why some of these fungi should not be considered members of a bolbitiaceous genus which are adopted to xerophytic conditions; a discussion of this problem is deferred to a later paper. However, the twelve species of this group which have been described have oscillated between the supposedly agaric genus *Cyttarophyllum* (Heim) Singer and the gastromycetoid genus *Galeropsis* Vel.

The great interest in these gastromycetoid fungi is attributed to the findings of similar transitional fungi between typical agaric genera and gastromycetes in other families of the Agaricales. It is probably understandable to find some of the gastromycetoid members of the family widely distributed, in both agaric genera e.g. *Bolbitius* and amongst the gastromycetes e.g. *Secotium*.

Although the genera of the *Bolbitiaceae* are well defined the species now placed in them have been attributed to a whole host of unrelated brown-spored and even purple-spored agaric genera. The majority have been distributed in either the very artificial genus *Pholiota* or in *Galera*, depending on whether the gills, before becoming exposed to the atmosphere, were protected by an annulus (*Pholiota*) or by a fugacious veil (*Galera*).

A review of the literature shows that members of the genus *Agrocybe* are also to be found in *Hebeloma*, *Psilocybe*, *Stropharia* and *Pratella* and members of the genus *Conocybe* in *Naucoria* and *Cortinarius*.

Due to nomenclatural misunderstandings many species, particularly of the genus *Conocybe*, have been placed in very obscure genera such as *Galerula*, genera often badly defined and untypified. Similarly species of *Bolbitius* have been placed in *Mycena*, a generic name more familiarly applied to a white-spored group of agarics.

Whilst it is easy enough to recognise the genera of the family, even in the field, differentiation of the species is frequently difficult and highly critical. The general facies exhibited in the genera is very constant and it is because of this homogeneity that much taxonomic confusion in the family has resulted. This is particularly true for the interpretation of the specific names proposed by early authors such as Fries (1821) and Persoon (1801). Because of this doubt about the identity of the fungi these early authors recognised, many of the records, particularly of *Conocybe* species, in the works of Massee, Cooke, Rea, W. G. Smith and others, must be abandoned. This is due to misinterpretation and/or poor documentation, and except for a few really distinctive species, the published records for the British Isles are of little value unless voucher specimens have been preserved and/or detailed notes of macro- and microscopic characters kept—preferably accompanied by a coloured illustration.

Bolbitius is a well defined genus and easily recognised in the field. The determination of the species within the genus presents but few difficulties, except in the tropical species. Many epithets are to be found in the literature but the distinctness of the fungi for which the names were given is questionable, even for those names based on West European collections. In *Agrocybe*, unlike *Conocybe*, there has been only a little confusion over the interpretation of the names proposed by Fries and his contemporaries. Except for a few instances old records are quite reliable and are of value but it is often useful to refer to herbarium material of such records when this is available, particularly when considering so-called polymorphic species.

In most agarics the number of possible taxonomic characters is very much smaller than in a comparably sized group of flowering plants. This makes taxonomic work on these fungi by no means easy; the matter is made even more difficult in the *Bolbitiaceae* by the very great similarities between groups of individuals which have been considered species.

A very similar situation is found in *Coprinus* but here the epicuticular ornamentation gives the best clues to specific separation. Even superficially similar collections can now be quite easily and definitely separated. In the genera of the *Bolbitiaceae* no such single character exists which can help in the classification, although in *Conocybe* Kühner's original separation into sections based on presence or absence, or type of caulocystidia, and distribution of hairs, is the most useful, after certain emendments and expansions have been carried out as will be further outlined below.

Unlike many of the higher fungi the family *Bolbitiaceae* is of little economic value to man. *Conocybe* and *Bolbitius* are worthless from a culinary point of view, although several *Agrocybe* species are considered delicacies e.g. *A. praecox* and *A. cylindracea*. The latter is cultivated by a semi-natural method in Southern Europe. *Conocybe cyanopus* has been shown by Benedict *et al.* (1962) to contain the hallucinogenic compound psilocybin and *C. siligneoides* is reported by Heim (1957) and Wasson (1961 and 1962) to be used by Mexican Indians in a similar way to mescalin.

Poisoning due to ingestion of fungi belonging to this family is unrecorded although during the present study intravenous injections of disintegrated mycelium of *Conocybe farinacea* brought about relapses in rabbits and over a six month period blindness and death. The active substances were not identified but they may be related to agrocybin, an antibiotic isolated from *Agrocybe dura* and named by Kavanagh, Hervey and Robbins (1950). Agrocybin is highly toxic and inactivated by blood. Bacteriostatic substances have been indicated as being present under certain conditions in carpophores of *A. aegerita* (=*cylindracea*) and *A. pediades*.

Carpophores of members of the *Bolbitiaceae*, particularly *Agrocybe*, collected in the field frequently contain insect larvae. Many of these have been identified as the larval stages of members of the *Mycetophilidae*.

Members of the *Bolbitiaceae* are non-mycorrhizal and grow on earth, sawdust, charcoal, old dung, worm-casts, vegetable debris, rotten wood, etc. They are found in woods, pastures, sand-dunes, gardens and greenhouses. No species is a proven parasite, although some, especially *Agrocybe* species, are xylophilous. Many have very definite ecological requirements.

The family is cosmopolitan, some species being found in north and south temperate regions and others in tropical and sub-tropical areas; some species are more widespread. A few groups have a very definite distribution e.g. *Conocybe* subgen. *Ochromarasmius* and *Agrocybe* subgen. *Aporus* (sect. *Velatae*), but a large amount of work has still to be carried out in order to find the world distributional limits of selected groups of species. Many isolated records exist for areas outside the north temperate regions but these in themselves do not give a complete picture.

The family *Bolbitiaceae* consists of about 250 described brown-spored agarics distributed throughout the world. The majority of the species of the constituent genera of the family have been described from north temperate regions of Western Europe (45 recorded from the British Isles, see Dennis, Hora and Orton, 1960) and the United States. This appears to be due solely to the lack of extensive collecting in more tropical countries. The recognition of even the temperate species, however, has been elucidated only in recent years. A much wider distribution of most species is indicated by reports now being made available of collections not only from the more remote tropical areas of the world but from the temperate regions as well. These records also suggest that many more species await collection and description. Care must be taken in interpreting these records, however, as there is little doubt that introduction into certain areas has taken place; this is probably particularly important with coprophilous species.

Velenovsky (1947) estimates that the number of species of *Galera* (*Conocybe* and *Galerina*) is of the order of 4,000 in Europe alone, whilst Singer (1951) admits not more than 204 (43 *Conocybe* species) in the world flora i.e. twenty times as few. This in itself poses an interesting problem, especially as the present study has shown that many of the members of the family can be examined in pure culture, both in the vegetative and carpophore stages.

A group of agarics such as the *Bolbitiaceae* in which there has been much taxonomic confusion, and many of whose members can be readily cultivated on partially sterilised substrata and obtained in pure culture, presents an excellent opportunity for investigating relationships by both classical and experimental methods. The two techniques are complementary and it is completely compatible to examine the members of the *Bolbitiaceae* experimentally whilst carrying out a revision of the nomenclature and taxonomy. Before such a formal monographic revision could be undertaken it was necessary to examine the stability and limitations of the taxonomic characters traditionally used in the understanding of the members of the family. The techniques and results of this experimental investigation will be discussed elsewhere.

Herbarium material of many members of the family *Bolbitiaceae* from Western Europe, N. America, Asia and Australasia has been examined during the course of the present study. The study of herbarium material has been supplemented by the examination of fresh material collected from all parts of the British Isles, especially from Kent and Surrey, the North, East and West Ridings of Yorkshire, Derbyshire, Co. Durham, the Lothians, Perthshire and Inverness-shire. Many of these areas are typified by calcareous or base rich soils e.g. chalk downs, limestone pastures and hill grazed spots on basic metamorphic rocks. The bolbitiaceous floras of grassland, fen, wood and scrub, at high and low altitudes have all been analysed.

ACKNOWLEDGEMENTS

The work, of which this is the second published result, could not have been undertaken without the help of the many mycologists who have placed their personal collections, knowledge and comments freely in my hands. I think it is appropriate in this introduction to the *Bolbitiaceae* to thank all these people; except in special cases these acknowledgements will not be repeated in future papers.

My thanks are due to the directors of Kew, British Museum, Leiden and Uppsala for loan of herbarium specimens; to Professor R. Kühner and Dr. A. F. M. Reijnders for valuable material and particularly to P. D. Orton who has put all his notes and specimens at my disposal. I must also thank Dr. M. A. Donk, L. Imler, Drs. C. Bas, Dr. R. A. Maas Geesteranus, Professor R. Heim, Dr. C. Rogerson, Professor H. Romagnesi, M. Herregods for information, helpful comment and exchange of reprints; Dr. J. Grainger who has placed his ecological notes at my disposal, and especially Dr. H. Fletcher and D. M. Henderson for critical review of the work, part of which was carried out when the writer held a research studentship granted by the Department of Scientific and Industrial Research.

TAXONOMIC ARRANGEMENT OF THE BOLBITIACEAE SUGGESTED IN THE PRESENT STUDY

Careful consideration has been given to all the characters which have been used to separate *Conocybe* and *Pholiotina*. *Galerella* acts as a smooth transition from *Conocybe* to *Pholiotina*. The presence or absence of dermatocystidia is not sufficient to separate the two genera for several undoubted *Conocybe* species possess them, e.g. *C. laricina*, and many referred to *Pholiotina* lack them—in fact they are very rare or absent in the type species of *Pholiotina: P. blattaria*. Developmental types are equally unreliable, certain *Pholiotina* species having just as fugacious a veil as a typical *Conocybe*, although it is true that no *Conocybe* is recorded (as yet) with a ring; the latter is a character confined to a fairly homogeneous group of species placed in *Pholiotina*. The cheilocystidia of *Conocybe* are typically lecythiform, a shape not found in *Pholiotina*, even though *P. brunnea* and *P. appendiculata* have distinctly capitate cells. This last fact, coupled with the characters of a reduced hymenophoral trama, would seem to give more justification for a separation of the two groups of species, but *Galerella* has a reduced trama yet no lecythiform cheilocystidia; in this genus the cheilocystidia are lageniform with a long drawn out neck. The reduction of the hymenophoral trama seems to be more related to ecological conditions, the reduction being greatest in those species which inhabit open environments. Thus all the key characters separating *Pholiotina* from *Conocybe* are connected by many intermediates, except for cheilocystidial shape which although distinct is considered insufficient and impracticable for separation at generic level. The plicate-sulcate striated pileus is not sufficient to separate *Galerella* from typical *Conocybe* since *C. umbonata** has this character.

Pluteolus is reduced to a subgenus of *Bolbitius*, a treatment favoured by but few authors since Quélet e.g. Ricken, Singer. The characters for generic separation are few, the chief one being the xylophilous habit. However, *Bolbitius vitellinus*, the type of the genus *Bolbitius*, is frequently found on wood chips and sawdust and uncommonly on rotten stumps. Similarly, some collections of *Pluteolus reticulatus* are humicolous and for these collections the name *P. dictyopus* has often been used in the past. Carpophores of species previously placed in *Pluteolus* do not appear to disorganise as rapidly as typical *Bolbitius* species but this is directly related to the thickness of the pileus flesh. The attachment of the gill to the stipe is not constant. Microscopically the two groups of fungi are very similar, e.g. in spore shape, structure, and cheilo- and pleurocystidial characters, except that collections attributable to *Pluteolus reticulatus* frequently have epicuticular hyphae amongst the hymeniderm elements. Several collections of true *Bolbitius* species have now been located with a similar or parallel character.

* **Conocybe umbonata** (Massee) Watling **comb. nov.** A full description will appear in a future paper. Basionym: *Bolbitius umbonatus* Massee in Kew Bulletin, 1906, 46.

Agrocybe as outlined by Singer (1936, 1951) has been retained with but few changes.

Kühner's sections in *Conocybe* subgen. *Conocybe* have been emended to take into consideration the experimental data obtained after the production of carpophores in pure culture in the laboratory. Although caulocystidial shape remains fairly constant, the presence or absence of hairs on the stipe and pileus is an unreliable character. Typical members of the *C. rickeniana* complex will produce hairs under certain conditions and members of the *C. silignea* group lack them. (See also Herregods 1952).

I consider it necessary to define two terms in relation to the *Bolbitiaceae* which will be used during this study.

1. HAIR—a single celled, very rarely 2–3 celled, hyaline or only faintly coloured, long sterile, filiform unit of the pileus and/or stipe very rarely greater than 4μ wide, not darkening in caustic alkali and unrelated to any cystidial element to be found in and on the same carpophore or carpophores of closely related species.

2. EPICUTICULAR HYPHA—a single or more celled, hyaline or only faintly coloured, sterile never specialised or filiform hypha of more normal width (usually greater than 7·5μ wide) not darkening in caustic alkali, unrelated to any cystidial element of the pileus in and on the same carpophore or carpophores of closely related species and not appearing to be a part of the hymeniform epicutis (=hymeniderm). The origin of the hypha may be sought in the fact that in young undifferentiated primordia the pileus is covered in a loose form of trichoderm (Reijnders, 1962).

BOLBITIACEAE Singer in Pap. Mich. Acad. Sci. 32, 147: 1946 (publ. 1948).

Basidia most frequently short and broad, two-spored and four-spored, typically the latter. Hymenophore lamellate, spore-print rich deep rust, rust-fuscous or hazel ± flushed dull brown; never with purplish tints and never black, ochraceous, pink, green or white. Basidiospores honey or rust under the microscope, smooth, much less frequently punctate or verrucose, usually with a broad or narrow germ-pore; always (?) darkening in solutions of strong alkali. Epicutis hymeniform often differentiated late in development and/or easily lost by damage. Pileocystidia less frequently present; caulocystidia widespread; hairs frequent. Cheilocystidia in all species thin-walled often morphologically complex, pleurocystidia absent or infrequent; brachycystidia not widespread. Stipe fleshy to fragile, central, infrequently elongated into a pseudorhiza. Pileus frequently quite small (mycenoid) more rarely very large (collybioid or tricholomoid), pulvinate and then fleshy or thin-fleshed and fragile, hygrophanous or not, expallent or not, less frequently viscid. Saprophytic on earth, sawdust, charcoal, old dung, vegetable debris, etc. Habitat woods, pastures, gardens and greenhouses.

TYPE GENUS: *Bolbitius* Fries

1. **Bolbitius** Fries, Epicrisis systematicus mycologici, 253 (1838).
Syn.: *Pluteolus* (Fries) Gillet, Champ. France Hymen. 549 (1876).
Agaricus subgenus *Pluteolus* Fr. Hymen. Europaei 266 (1874).

Agaricus subgenus *Galera* sect. *Pluteotropi* Fr. Mon. Hym. Sueciae 387 (1875).

also *Mycena* (Pers.) Rousell as used by W. A. Murrill (1917) in North American Flora, 10(1): 190, New York.

Habit coprinoid. Pileus viscid, plicate-sulcate or with sulcate margin; pileocystidia absent; epicuticular hyphae sometimes present. Stipe central, punctate or floccose striate, frequently white; caulocystidia present. Gills at first ascending then oblique developing rapidly and decomposing after spore-dispersal, thin, rich rust; cheilocystidia present, pleurocystidia not infrequent; brachycystidia prominent; hymenophoral trama regular but often becoming alveolate. Carpophore pigment frequently cystochroic and brightly coloured. Spore-print rich rust-brown. Basidiospores smooth, with prominent germ-pore, darkening in aqueous alkaline solutions. Development apparently paravelangiocarpic. Clamp-connections rare or completely absent; sexuality unknown, ? homothallic. Habitat as in the family, frequently distinctly xylophilous or attached to herbaceous remains.

TYPE SPECIES: *Agaricus vitellinus* Pers. per Fr., selected.

A. vitellinus was the first species in Systema mycologicum (1821) of all those now attributable to *Bolbitius* but placed by Fries at that time in *Agaricus*. It is also the first species listed under *Bolbitius*, in Fries's subsequent publications. (See Singer (1936, 1951, 1962) and Singer and Smith (1946) where *Agaricus fragilis* Linn. per Fr. is selected as type species. *A. fragilis* is here considered a synonym of *A. vitellinus*).

Note: Those entries with an asterisk (*) are alterations to Singer's current scheme of classification as outlined in his book "The Agaricales in Modern Taxonomy" Ed. 2, 1962. Those entries with a dagger (†) are alterations to the nomenclature outlined in the same publication.

*subg. 1. **Bolbitius** Fries.

*subg. 2. **Pluteolus** (Fries) Watling **nov. comb.**

Basionym. *Agaricus* subgen. *Pluteolus* Fr.

Type: *Agaricus reticulatus* Persoon per Fries already selected as type of the genus *Pluteolus*.

2. **Conocybe** Fayod in Ann. Sc. Nat. Ser. 7, 9: 357 (1889).

Syn.: *Pholiotina* Fayod, loc. cit. 359 (1889).

Galerella Earle in Bull. N.Y. Bot. Gdn. 5: 422 (1908).

Togaria W. G. Smith pro parte, British Basidiomycetes, 122 (1908).

Also in part *Galera* (Fries) Kummer auct. pl. and in part *Galerula* Karsten.

? *Meliderma* Velenovsky sensu Melzer in České Houby, 399 (1920).

Habit often mycenoid less frequently larger. Pileus hygrophanous or expallent, greasy or moist, less frequently viscid, often glistening when dry or becoming wrinkled, usually striate, slightly sulcate or not, more rarely plicate-sulcate; pileocystidia and hairs not uncommon. Stipe usually striate or fibrillose silky, frequently fragile, nearly always straight and central, villose, pubescent or pruinose, white or coloured; caulocystidia frequently specialised. Gills adnate, linear, lanceolate, less frequently free or with tooth, at first usually strongly ascending; cheilocystidia always present, often very specialised; pleurocystidia absent; brachycystidia infrequent; hymenophoral trama either reduced to a very thin mediostratum with an enormous hymenopodial development or mediostratum, although small, quite distinct. Carpophore pigment usually mesochroic. Spore-print rust-brown. Basidiospores with or without germ-pore, smooth, much less frequently punctate or verrucose, darkening in aqueous alkali solutions. Development appears to be para- or gymnovelangiocarpus. Sexuality appears to be either bipolar and heterothallic or of a secondarily homothallic type. Habitat as in the family.

TYPE SPECIES: *Galera tenera* (Schaeffer per Fries) Kummer, fixed by conservation.

The International Botanical Congress held at Stockholm in 1950 agreed to the conservation of *Conocybe* Fayod over *Pholiotina* Fayod, published on the same day, as well as over *Raddetes* Karsten (Hedwigia 26, 112, 1887), now thought to be a genus of gastromycetoid fungi with bolbitiaceous affinities, and over *Pholiotella* Spegazzini, shown by Singer to be based on a geophiloid agaric, probably a species of *Psilocybe*.

subg. 1. **Conocybe**

sect. 1. **Conocybe**

*Syn.: Section *Mixtae* Kühner ex Singer, pro maiore parte, 1962.

sect. 2. **Pilosellae** Kühner ex Singer in Sydowia, 15: 69 (1962).

Type: *Conocybe pilosella* (Persoon per Fries) Kühner, by original designation on validation.

sect. 3. **Candidae** Kühner ex Singer l.c. 69.

Type: *Conocybe lateritia* (Fries) Kühner sensu Kühner (= *Conocybe lactea* (J. Lange) Metrod), by original designation on validation.

sect. 4. **Gigantae** Singer in Sydowia, 2: 36 (1948).

Type: *Conocybe intrusa* (Peck) Singer, by original designation (sphalm. *C. destrusa*).

subg. 2. **Ochromarasmius** Singer in Mycologia, 39: 88 (1947).

Type: *Naucoria juruensis* P. Henning, by original designation.

*subg. 3. **Galerella** (Earle) Watling **nov. comb.**

Basionym: *Galerella* Earle, 1909.

Type: *Agaricus coprinoides* Peck non Corda (= *Agaricus plicatella* Peck), by original designation.

*subg. 4. **Pholiotina** (Fayod) Kühner.

Basionym: *Pholiotina* Fayod, 1889.

Type: *Pholiota blattaria* (Fries) Quélet, by original designation.

sect. 1. **Pholiotina** (Fayod) Kühner.

sect. 2. **Vestitae** Watling.†

Type: *Conocybe vestita* (Fr.) Kühner.

*subg. 5. **Piliferae** (Kühner ex Singer) Watling **nov. comb.**

Basionym: *Conocybe: Piliferae* Kühner 1935 *nom. nudum.*
Pholiotina: Piliferae Kühner ex Singer, 1950 *nom. nudum.*

Type: *Conocybe pygmaeoaffinis* (Fr.) Kühner s. Kühner, Singer by original designation on validation.

3. **Agrocybe** Fayod in Ann. Sc. Nat. Ser. 7, 9: 358 (1889).

Syn.: *Cyclopus* (Quélet) Barbier in Bull Soc. Sci. Nat. Sôane et Loire II, 33: 131 (1907).
Togaria W. G. Smith pro parte, British Basidiomycetes, 122 (1908).
Togaria W. G. Smith emend. Romagnesi in Rev. Mycol., 2: 178 (1937).
Bulla Batt. ex Earle in Bull. N.Y. Bot. Gdn., 5: 424 (1909).
Pseudodeconica van Overeem in Bull. Jardin Bot. Buitenzorg, 9: 19 (1927), *Nomen nudum* fide Singer (1951).

Habit collybioid or sometimes tricholomoid. Pileus often comparatively fleshy, not plicate-sulcate, less frequently striate; hairs sometimes present, pileocystidia absent (always?). Stipe central, frequently connected at base to rhizoids, uncommonly attached to sclerotia, often fleshy, white or coloured, roughened or smooth; caulocystidia present. Gills adnate, broad, usually snuff or fuscous-brown, often becoming more sordid, fairly broad; cheilocystidia always present; pleurocystidia very frequently absent, when present often very specialised; hymenophoral trama regular, often quite thick. Spore-print hazel or fuscous brown. Basidiospores smooth, with or without germ-pore, darkening in aqueous alkali solutions. Development apparently paravelangiocarpic. Sexuality apparently bipolar and heterothallic or of a secondarily homothallic type. Habitat various, more frequently on wood and agricultural land than other members of the family.

TYPE SPECIES: *Pholiota praecox* (Persoon per Fries) Kummer, by original designation (as *Naucoria praecox*).

subg. 1. **Agrocybe**

sect. 1. **Agrocybe**

sect. 2. **Pediadeae** (Fries) Singer in Beih. Bot. Centralbl. 56 B: 165 (1936).

Type: *Agrocybe pediades* (Persoon per Fries) Fayod by original designation. This species is considered by many authors as conspecific with *Agrocybe semiorbicularis.*

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† Section **Vestitae** Watling **sectio novo.** Pileus hygrophanus, siccus, subinde paulum humidus, laevis vel subtiliter pubescens propter pileocystidias, interdum praeditus fibrillis vel squamis minutis ad aciem propter albidos vel ochraceos flocculos vel cum velo appendiculato. Annulus absens. Pleurocystidia absentia, cheilocystidia fere elongato-utriformia altera elongato-clavata ad apicem semper obtusa, etiam lageniformia vel inaequaliter subcapitata vel distincte capitata sed tum numquam lecythiformia; caulocystidia similia. Typus: *C. vestita* (Fr.) Kühner.

†sect. 3. **Microsporae** Singer ex Singer in Sydowia 15: 69 (1962).

Type: *Agrocybe tuberosa* (P. Henning) Singer, by original designation.

†subg. 2. **Aporus** Singer ex Singer, loc. cit., 69 (1962).

Type: *Agrocybe aegerita* (Brig.) Singer (=*Agrocybe cylindracea* (DC. ex Fr.) R. Maire), by original designation.

†sect. 1 **Aporus** Singer ex Singer, loc. cit. 69 (1962).

sect. 2. **Velatae** Singer in Sydowia 2: 36 (1948).

Type: *Agrocybe erebia* (Fries) Kühner, by original designation.

sect. 3. **Evelatae** Singer in Sydowia 2: 36 (1948).

Type: ‡*Agrocybe firma* (Peck) Singer, by original designation.

KEY TO THE GENERA, SUBGENERA AND SECTIONS OF GENERA IN THE BOLBITIACEAE

1a. Gills free or adnate then becoming free; pileus viscid, thin and soon decomposing, almost deliquescent. Carpophore often brightly coloured; red, purplish or chrome yellow. Growing on wood, soil or herbaceous debris . . . . *Bolbitius* Fr. (2)

1b. Gills rarely free and, if so, then pileus never viscid, thin and deliquescent. Carpophore rarely brightly coloured, never pastel shades 3

2a. Typically growing on dung, herbaceous debris, sawdust, etc., less frequently on bare soil or directly on wood. Pileus hymeniderm usually lacking epicuticular hyphae. Gills ± free . . subgen. *Bolbitius*

2b. Typically growing on wood less frequently on bare soil, and herbaceous matter. Pileus hymeniderm with epicuticular hyphae amongst the hymeniderm elements. Gills free . subgen. *Pluteolus* (Fr.) Watling

3a. Spore-mass buff, hazel or cigar brown, spores smooth, usually with distinct germ-pore; carpophores with distinct or fugacious ring or with ± ring-zone. Medium to large, less frequently small agarics *Agrocybe* Fayod (4)

3b. Spore-mass rust brown or ochraceous rust, spores usually smooth less frequently punctate, usually with distinct germ-pore; carpophores ± annulate, cortinate or lacking veil remnants when mature. Medium to small agarics, pileus rarely over 25 mm . . *Conocybe* Fayod (9)

4a. Spores often truncated with distinct often broad germ-pore and distinct apiculus. Carpophores never dark brown or lignicolous, with or without distinct membranous ring . . . . subgen. *Agrocybe* (5)

4b. Spores not generally distinctly truncate, usually with indistinct germ-pore or germ-pore entirely absent. Carpophores humicolous and terricolous or lignicolous with or without ring or ring-zone, often dark brown and then with sub-boletoid shaped spores subgen. *Aporus* Singer (7)

5a. Veil well developed either as membranous ring or as appendiculate skirt to the pileus margin. Cheilo- and pleurocystidia present sect. *Agrocybe* (=*Praecoces* Singer)

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‡ See taxonomic discussion page 303.

5b. Veil otherwise. Lacking a distinct ring 6

6a. Veil extremely fugacious, frequently none or, when present, rarely forming floccules at the pileus margin or forming a distinct ring-zone; pleurocystidia none or sparse. Spores more than 10μ in length sect. *Pediadae* (Fr.) Singer

6b. Veil absent or extremely fugacious and leaving no evidence of previous existence in mature carpophores; pleurocystidia present; spores usually less than 10μ in length . . sect. *Microsporae* Singer

7a. Carpophore annulate, lignicolous. Ring membranous; spores never elongate and never greater than 10μ in length sect. *Aporus* Singer

7b. Not as above, veil either absent or, if forming a ring, not lignicolous 8

8a. Carpophores annulate, hygrophanous, humicolous never lignicolous. Spores elongate almost sub-boletoid in shape sect. *Velatae* Singer

8b. Carpophores never annulate, veil absent or, if present in young specimens, leaving no evidence in mature carpophores, humicolous seldom lignicolous. Spores never elongate, usually less than 10μ in length sect. *Evelatae* Singer

9a. Cheilocystidia distinctly lecythiform 10

9b. Cheilocystidia lageniform, fusiform, utriform, capitate, subcapitate but never symmetrically lecythiform 14

10a. Spores distinctly punctate or minutely roughened subgen. *Ochromarasmius* Singer

10b. Spores always smooth . . . subgen. *Conocybe* (11)

11a. Carpophore large, never smaller than 25 mm, with aspect of a *Cortinarius* or *Hebeloma* sp.; stipe white, distinctly bulbous covered in lecythiform caulocystidia; spores less than 8μ in length sect. *Gigantae* Singer

11b. Carpophores never as large; spores frequently larger than 8μ; stipe bulbous or equal; lecythiform caulocystidia often present, but when present in large numbers stipe never white 12

12a. Stipe white throughout life-cycle, pileus usually pale coloured also; stipe covered in short hairs and/or non-capitate caulocystidia sect. *Candidae* Kühner ex Singer

12b. Stipe never white throughout life-cycle and pileus usually more strongly coloured. Caulocystidia either lecythiform or not, hairs ± present 13

13a. Stipe with lecythiform caulocystidia throughout or limited to apex and/or base . . . . sect. *Conocybe*

13b. Stipe lacking lecythiform caulocystidia . sect. *Pilosellae* Kühner ex Singer *emend.* Watling

14a. Pileus plicate-sulcate, striate, cheilocystidia lageniform with long elongated neck; hymenophoral trama distinctly reduced subgen. *Galerella* (Earle) Watling

14b. Cheilocystidia never shaped as above or, if so, rarely and then pileus not plicate-sulcate, striate. Hymenophoral trama regular . . 15

15a. Pileocystidia always present, resembling caulo- and cheilocystidia, stipe white never becoming umber brown, black or rust, never annulate or with appendiculate veil, in fact infrequently showing evidence of veil subgen *Piliferae* (Kühner ex Singer) Watling

15b. Pileocystidia ± present, frequently not resembling those on the gill-edge; stipe black, umber, brown or rust often silky fibrillose and then appearing streaky white, distinctly annulate or veiled subgen. *Pholiotina* (Fayod) Kühner (16)

16a. Pileocystidia frequently lacking; stipe annulate sect. *Pholiotina* (Fayod) Kühner

16b. Pileocystidia ± present; stipe non-annulate but veil remnants evident as particles distributed on the pileus surface or as appendiculate veil and/or ring zone . . . . sect. *Vestitae* Watling

RELATIONSHIPS WITH OTHER AGARIC GENERA

i) **Simocybe** Karsten, 1879 and **Naucoria** Fayod, 1889.

The present study does not include any agaric which has been placed previously in the genus *Simocybe* Karst. as understood and extended by Singer, even though Romagnesi (1962) recently transferred the West European species of this genus to *Agrocybe*, and Fayod had linked the main genera of the *Bolbitiaceae* with his genus *Naucoria* (non Fries), which is probably equivalent to *Simocybe*.

a) *Simocybe* (= ? *Ramicola* Vel. 1929; em. Kühner and Romagnesi 1953),* according to Singer (1951) is mainly a tropical genus characterised by carpophores usually with an olivaceous overall coloration, an epicutis composed of erect hyphae with numerous dermatocystidia, a spore-mass usually with an olive tint, and with basidiospores reniform-phaseoliform to ellipsoid, with a callus (no germ-pore), and wall separable into more or less distinct endo- and episporia.

Singer has a first hand knowledge of many of the tropical agarics he attributes to this genus whereas Orton (1960), basing his observations on West European material only, discussed in full the limits of the genus *Naucoria* as understood by him and included *Simocybe* within its circumscription. The main fact which induced Orton to combine these two genera, considered so distinct by Singer, was that he had found four agarics which combined the characters of both genera.

The following points must be considered before Romagnesi's emendments of the genus *Agrocybe* and proposals for *Simocybe* are accepted.

(1) BASIDIUM: The morphology of the basidia of *Naucoria rubi* (=*haustellaris*) and *N. sumptuosa* does not agree with that of basidia of members of the *Bolbitiaceae*; they are not typically short and broad.

(2) BASIDIOSPORES: The basidiospores of *Conocybe vestita* and of the *Agrocybe erebia* complex are aporate and many species of both *Conocybe* and *Agrocybe* have either small or indistinct germ-pores e.g. *Conocybe togularis*, *C. mairei*

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* The only original species of this genus, and therefore the type is *R. olivacea* Vel. Favre (1948) considers that probably *R. olivacea* is nothing but a form of *Naucoria centunculus*.

and *C. pilosella*. Thus it would not be difficult to emend the *Bolbitiaceae*, however artificially, to include agarics whose basidiospores had a callus in place of a true germ-pore; but when other morphological characters of the basidiospores, particularly shape and parietal structure, are taken into account, Romagnesi's group and the *Bolbitiaceae* appear to be distinct (see also Singer 1951).

The basidiospores in both groups are smooth. In most species of the *Bolbitiaceae*, ultra thin sections of the spore wall fails to show a distinct episporium and exosporium, a feature which Singer characterises for the basidiospores of members of the genus *Simocybe*.

Whereas basidiospores of members of the *Bolbitiaceae* undergo a darkening with alkali, no change was recorded using the basidiospores of *Naucoria rubi* and *N. sumptuosa*, two species Romagnesi transferred to the genus *Agrocybe*.

(3) COLOUR OF THE SPORE-PRINT: Still usually considered important in the classification of the agarics, spore-print colour must be carefully considered when discussing Romagnesi's suggestions. In the *Bolbitiaceae* olivaceous tints are absent from the colour of the spore-mass whereas, in *Simocybe*, it is cigar to snuff brown, frequently with an olivaceous cast (Ridgway: Buffy brown to Citrine Drab). The colours exhibited in the spore-print of *Simocybe* are never as russet as those in *Bolbitius* and *Conocybe*, although some *Simocybe* species that lack olivaceous tints have spore-mass colours which approach those of *Agrocybe* (Watling 1964 for Ridgway equivalents).

(4) CYSTIDIA: The cheilocystidia exhibited by the species in Romagnesi's group do not resemble those most frequently found in members of the *Bolbitiaceae* of comparable carpophore size, i.e. with *Conocybe*. They are never lecythiform and approach most closely those found in members of the genus *Agrocybe*.

Pleurocystidia are present in *Agrocybe*, except in certain members of subgen. *Agrocybe* (sect. *Pediadeae*); they are absent in other members of the *Bolbitiaceae* or exceedingly rare in *Bolbitius* as they are in the five taxa transferred to *Agrocybe* by Romagnesi.

(5) MACROSCOPIC CHARACTERS OF THE PILEUS: Pileus striation is absent in the majority of *Agrocybe* species except in old specimens and when developed it is not prominent. In *Conocybe* it is very frequently present although closely related species often show varying degrees of striation. In this character the pileus of members of the *Naucoria centunculus* group conform for they are not or scarcely striate when moist or striate only at the margin. In the colour of the pileus flesh, however, they differ from the *Bolbitiaceae* in having an olive brown, a greenish olive or a snuff-brown hue. In those agarics, transferred by Romagnesi to *Agrocybe*, all are typified by a velvety-pruinose pileus surface, a character not shared by the *Bolbitiaceae*.

(6) PILEUS EPICUTIS: In the group of agarics he transfered to *Agrocybe* Romagnesi described a "cellular cuticle" only for *Naucoria centunculus*, N. *centunculus f. filopes* and *N. sumptuosa* (=*N. centunculus f. luxurians*); the other taxa he transferred were *N. haustellaris* (=*N. rubi* of the New Check List) and *N. coniophora*.

The *Bolbitiaceae* is characterised by a hymeniform epicutis, although, when examining members of the genus *Agrocybe*, it was observed that the hymeniform epicutis often differentiates late in the development of the primordium and frequently may be destroyed on further expansion of the pileus. However, a "cellular cuticle" is not confined in the brown-spored agarics to the *Bolbitiaceae* for Orton (1960) has described *Naucoria celluloderma* with truly subglobose cells in the cuticle. *N. celluloderma* however, has elongate-limoniform punctate-rough basidiospores characteristic of *Naucoria;* such a combination of characters is rare. In the *Bolbitiaceae* the important point is that the "cellular cuticle" is closely related to the hymenium i.e. it is a hymeniderm.

Examination of the type material shows that *N. sumptuosa* has really a heterocellular cuticle, i.e. rather broad and short cells present together, and cannot be considered a hymeniform epicutis. Thus it only resembles superficially the epicutis of members of the genus *Agrocybe* but obviously many more careful observations are required particularly on tropical material. The velvety-pruinose character of the pileus of *N. centunculus* is due to the presence of lageniform or clavate fusiform pileocystidia. Dermatocystidia, such as this are found in few members of the *Bolbitiaceae*, usually being replaced by the unrelated filiform hair. Pileocystidia when present are found most frequently in members of *Conocybe* subgen. *Pholiotina*, particularly sect. *Piliferae*. They are, however, extremely closely related in structure to the cheilocystidia whereas the dermatocystidia in *N. sumptuosa* and related species are rather different in shape, size and differentiation to those on the gill edge. In *Agrocybe* pileocystidia are rare or certainly uncommon, even though some members of the genus have hairs or irregularly distributed epicuticular hyphae present in the epicutis. *A. firma*, however, is an exception to this general theme for it agrees more with the *N. centunculus* group in possessing similar pileocystidia.

The pigmentation of the hyphae of the pileus cortex in *Simocybe* is both mesochroic and ectochroic; encrusted hyphae are never found in members of the *Bolbitiaceae*.

(7) HYMENOPHORAL TRAMA: The structure of the hymenophoral trama of members of the *N. centunculus* group is similar to that of many members of the *Bolbitiaceae* particularly those placed in the genus *Agrocybe*.

(8) DEVELOPMENT: All the members of the *Bolbitiaceae* so far examined (Reijnders 1948, 1952, and 1963, Watling 1963 and 1964) possess paravelangiocarpic development whereas the few naucorioid species studied by Reijnders (1948 and 1963) have been either monovelangiocarpic or bivelangiocarpic, excepting *N. centunculus* which is paravelangiocarpic. This is an interesting situation supporting Romagnesi's suggestions; further careful analysis is required.

(9) HABITAT: Members of the *N. centunculus* group grow either directly on woody or rotten plant debris, or about stumps or trunks. The xylophilous habit in the *Bolbitiaceae* is uncommon; important exceptions are *Agrocybe cylindracea* and sometimes *A. praecox*, *Pluteolus reticulatus* and *Conocybe laricina*. *A. firma* in its ecological characters agrees with the *N. centunculus* group, particularly its variety *attenuata* Kühner, which Orton has raised to specific rank (1960).

CONCLUSION: There is little doubt Romagnesi has detected an interesting and probably very accurate relationship. Further work is required on *A. xuchilensis* and *A. xerophytica*, that is, other members of *Agrocybe* sect. *Evelatae*. *A. vervacti* is certainly a true *Agrocybe*. *A. firma* in its original sense may also be! However, North American specimens may not agree completely with the current interpretation accepted for this same species in Europe (e.g. Kühner and Romagnesi, 1953). I await the examination of type material and it is because of this I have retained the sect. *Evelatae*. In event of discordances between herbarium material from Europe and America for *A. firma*, it will be necessary to retain sect. *Evelatae* minus *A. firma*, the section's type, under a separate name and transfer *A. firma* to *Simocybe*.

Apart from *A. firma* the limits between *Simocybe* and the genus *Agrocybe* appear to be quite distinct. However, careful examination of the tropical species which have been attributed to the genus *Simocybe* must be made before these distinctions can be fully appreciated.

b) Fayod (1889) under his sixteenth tribe, the "Naucoriés", included "*Naucoria* nob., *Conocybe* nob., *Bolbitius*, *Agrocybe* gen. nov., *Pholiotina* gen. nov. and *Rozites* Karst." He stated that the tribe differs from the "Tubariés", i.e. *Galera*, *Flammula*, and *Tubaria*, by the presence of a usually persistent, cellular cuticle to the pileus, a stipe medulla and a distinct germ-pore and endospore wall to the basidiospore. The tribe Naucoriés consists of the major part of Fries's *Naucoria* and *Galera* and some *Pholiota* species. The members of the tribe furthermore were stated to be geophilous and subangio- to angio-carpic in their carpophore development.

Naucoria is considered by Donk to denote a radical emendation or restriction by Fayod of *Naucoria* Fries and not a "new" name for a group of organisms. However, it can be argued that Fayod envisaged a completely different group to that of Fries. Fayod like many other authors, e.g. Karsten, considered Fries's *Agaricus* trib. *Naucoria* to be heterogeneous and wished to clear up the problems involved before he fitted these brown-spored agarics into his scheme of classification. Fayod included in his genus, in fact as type, *Naucoria cerodes*, a fungus not included amongst *Naucoria: Genuini* by Fries in 1821; he also included in his genus *N. melinoides*, a fungus placed by Fries in *Galera* in 1821, and *N. vervacti* a fungus which is now placed in *Agrocybe*, although formerly placed by Fries in *Naucoria: Phaeoti*, a group later destined to be temporarily excluded from *Naucoria* by even Fries himself (1828).

Naucoria melinoides is considered by Dennis, Hora and Orton (1960) in its original sense to be "a doubtful species". In the sense of Ricken (1915) it is undoubtedly *N. escharoides* (=*Alnicola*), but in the British Isles the epithet has frequently in the past been applied to the common, uniformly dull honey-coloured agaric *Galerina moniophila*. Thus Fayod excluded all the agarics that Fries considered to belong to *Naucoria: Genuini* (=*Lepidoti*); Fayod therefore must be considered as creating a new genus of agarics using an old name. Misinterpretation by Fayod of *N. melinoides* in a similar way as Ricken later did, could, it is true, have occurred but this would not appear to be the case for *N. escharoides* has a distinctly "heterocellular cuticle" and Fayod was careful about the wording of his generic diagnoses.

Kühner (1926) created the genus *Alnicola* and *N. melinoides* has been selected as the type of the genus; in this case also *N. melinoides* is synonymous with *N. escharoides*.

Naucoria is differentiated from *Conocybe* by Fayod on the structure of the hymenophore and its constituents stating that members of the former genus have an indistinct subhymenium, skittle-shaped cystidia and spores with a poorly pronounced hilar depression and germ-pore; *Conocybe* had, on the other hand, a well-developed subhymenium and germ-pore to the basidiospores but lacked a hilar depression.

It must be noted in passing that Fayod included *Galera pygmaeoaffinis* in his tribe Tubariés under the genus *Galera* which according to him lacks a "cellular cuticle". This may support some authors who feel that *G. pygmaeoaffinis* as interpreted currently may not be correct, i.e. interpreted in the sense of Fries.

Rozites is said by Fayod to differ from *Pholiotina* by the cellular cuticle being many layered and dry and the basidiospores being punctate with a germ-pore papilla. *R. caperata*, however, has a cuticle composed of repent cells, often quite thick, but quite definitely filamentous. *Rozites* cannot therefore be considered to be close to either *Conocybe* or *Agrocybe*.

CONCLUSION: Although in 1879 Karsten had described the genus *Simocybe* to cover *Naucoria: Gymnoti* and *Phaeoti*, I consider Fayod like him had seen the necessity to split the Friesian tribe *Naucoria*. Like Romagnesi I feel Fayod also saw the close connection (superficial as it may be) between certain naucorioid agarics and certain members of the *Bolbitiaceae*.

ii) **Panaeolus** (Fr.) Quélet.

Kühner and Romagnesi (1953), in some ways rather surprisingly, placed *Panaeolus* (including *Anellaria* and the related *Panaeolina*—a concept supported by the present author) in the *Bolbitiaceae*. Recently however, Romagnesi (1962) has suggested *Panaeolus* is better placed close to *Geophila* Quél., i.e. *Stropharia* and *Psilocybe*. The genus *Panaeolus* certainly comes close to the *Bolbitiaceae* as here understood, in habitat preference, development, and in possessing a "cellular cuticle". But because the spore-mass is black, dark brown or deep purple-fuscous and the cystidia are slightly different in structure, the genus is here excluded from the family and included in the *Coprinaceae* sub-family *Panaeoliodeae* as recommended by Singer, although with little conviction.

The connection between *Panaeolus* and the *Bolbitiaceae* will be frequently discussed for there are several facts in favour of Kühner and Romagnesi's placing and these are examined below.

1) DEVELOPMENT: The paravelangiocarpic development of the *Panaeolus* group (Reijnders 1948, 1952, and 1963) (personal observations on five *Panaeolus* species, and the single W. European species of *Panaeolina*) is parallel to the development found in the *Bolbitiaceae*; the other members of the *Coprinaceae* are bi- or monovelangiocarpic (Reijnders, see above and personal observations on seven *Coprinus* species).

The patchwork maturation of the basidiospores on the gills, typical of *Panaeolus* (Buller's *Panaeolus* subtype (1924)), has not been found in the *Bolbitiaceae*.

2) BASIDIA: The basidia of most *Panaeolus* species are fairly short and broad and therefore conform in general to the characteristic shape of the basidia of the *Bolbitiaceae*, particularly those with regular, more fleshy trama, e.g. *Agrocybe* species.

3) BASIDIOSPORES: The structure of the basidiospores in *Panaeolus* is very close to that of the *Bolbitiaceae*. *P. foenisecii* has ornamented spores but so too have some *Conocybe* species, e.g. *C. laricina* and *C. martiana*. The shape of the spore in *Panaeolus* is typically limoniform but some species have the ovate-elliptic spore so characteristic of the *Bolbitiaceae*. The limoniform-sublimoniform spore it is true is uncommon in the *Bolbitiaceae* but such shapes are approached very closely in certain *Conocybe* species, e.g. *C. antipus*, *C. hexagonospora* and others as yet undescribed. As in many members of the *Bolbitiaceae* a large germ-pore is typical of the *Panaeolus* spore.

4) COLOUR OF SPORE-PRINT: This is the most noteworthy feature separating *Bolbitius* and *Conocybe* from *Panaeolus* for, in the last genus, the spore-print is black with faint umber or purplish flush (Ridgway: Fuscous black to Blackish green-grey). Such a colour is unknown in the *Bolbitiaceae*. However, it may be that spore colour in this case has influenced us far too much, and biased the judgment as to the importance of other characters.

5) CYSTIDIA: All *Panaeolus* species possess cheilocystidia and caulocystidia and some have sparsely distributed pileocystidia (see below). The caulocystidia resemble the cheilocystidia in form and structure and those of members of the *Bolbitiaceae*. *P. semiovatus* and *P. ater* possess pleurocystidia which have an internal, deeply staining body. Such structures in the cystidia are unknown in the *Bolbitiaceae* but as yet I am not convinced that these have exactly the same origin as the true chrysocystidia of members of the *Strophariaceae*.

6) MACROSCOPIC CHARACTERS OF THE PILEUS AND VEIL: The outward appearance of the pileus in *Panaeolus* is very similar to that of many *Agrocybe* and *Conocybe* species. The veil in *Panaeolus*, as in the *Bolbitiaceae* is either present as an appendiculate veil, e.g. *P. sphinctrinus*, or a ring or ring-zone, e.g. *P. semiovatus*, or is completely fugacious. I do not therefore place much emphasis on this character.

7) PILEUS EPICUTIS: In both the *Bolbitiaceae* and the *Panaeoloideae* the epicutis is hymeniform. Just as in the *Bolbitiaceae*, particularly subgen. *Pholiotina*, some *Panaeolus* species, e.g. *P. ater*, possess an epicutis with sparsely distributed pileocystidia. These pileocystidia resemble the cheilo- and caulocystidia of the *Bolbitiaceae* in shape and structure, although in some specimens of *Panaeolus* they are possibly thicker walled and yellow coloured. A similar yellow coloration is found in the pileocystidia of *C. laricina*. Like Hora (1957) I am unable to support the dismemberment of *Panaeolus* based on differences in structure of the pileus as outlined by Godfrin (1903).

8) HYMENOPHORAL TRAMA: The structure of the hymenophoral trama in *Panaeolus* agrees with that of many members of the *Bolbitiaceae*, particularly those placed in the genus *Agrocybe*.

9) BIOCHEMISTRY: It is interesting to note that certain *Panaeolus* spp. and *Conocybe cyanopus* show the ability to produce psilocybin (Benedict *et al.* 1962).

10) CULTURAL CHARACTERS: *Panaeolus campanulatus, P. sphinctrinus, P. acuminatus, P. papilionaceus, P. fimicola, P. semiovatus* and *P. foenisecii* have all been cultured during the present study to assess cultural differences between the *Coprinaceae* subfam. *Panaeoloideae* and the *Bolbitiaceae*. In contrast to the latter, the mycelium of the *Panaeoloideae* can be easily reisolated from dung and the basidiospore germination is always very high (75% for most *Panaeolus* species as against 25% for the majority of cultivable *Conocybe* species and up to 50% in *Agrocybe*). On all nutrient agars examined the colonies of *Panaeolus* are more velvety and the rate of growth is up to ten times as fast. Sclerotia and rhizoids are not formed.

11) HABITAT: Ecologically the *Panaeoloideae*, growing directly on dung or in richly manured soil, are more strictly coprophilous than most members of the *Bolbitiaceae*. Their pH tolerance, however, is much the same as that of *Conocybe* (pH rarely less than 5·5, average 7·25; only exception *Conocybe coprophila* pH 4·5–5·75), from over fifty pH readings of the soil about the base of carpophores of *Panaeolus* species the range was 5·0 (two collections: *Panaeolus retirugis* and *P. semiovatus*)—8·0 (two collections: *P. semiovatus* and *P. sphinctrinus*): average value 6·5, commonest values 6·0, 7·0 and 7·5. Collections of *P. foenisecii* agree with these observations.

CONCLUSIONS: There appears to be some very real connection between the *Panaeoloideae* and the *Bolbitiaceae*. We must in the future be very careful of not overemphasising the difference between the spore-print colours of these two groups of agarics. After the examination of New World species and, in the light of the above facts, a reassessment of the affinities between the *Bolbitiaceae* and this black-spored subfamily will be most instructive.

iii) **Strophariaceae**

In the present work the family *Bolbitiaceae* has been defined as a group of brown-spored agarics with a strictly hymeniform epicutis. If this character, which the author believes is fundamental, is not taken into consideration then some members of the *Strophariaceae* appear to approach in their morphology certain bolbitiaceous agarics, particularly those placed in the genus *Agrocybe*. Singer has traced the origin of the idea of placing these two groups of agarics close to each other to a publication by Van Overeen (1927). This latter author classified *Stropharia* and *Phaeodeconica* (=*Agrocybe* fide Singer) in the family *Strophariaceae*. There is little doubt Van Overeen's reason for the placing of this group of typically purple-spored agarics with a brown-spored group was based in part on the superficial similarity in nacroscopic characters between certain members of *Agrocybe* and *Stropharia*, e.g. *Agrocybe semiorbicularis* and *Stropharia semiglobata* and *A. praecox* and *S. coronilla*. However, all members of the *Strophariaceae* have a filamentous "cuticle".

If *Agrocybe* were to be placed in the *Strophariaceae* as it is at present understood it would be placed, because of the spore-print colour of its members, along with *Pholiota, Kuehneromyces* in the *Pholiotoideae* (the *Stropharioideae* is characterised by spore-prints of a deep lilac blackish or deep fuscous sepia, with purple hue). Singer, linked the *Strophariaceae* to the *Bolbitiaceae* through the secotiaceous genus *Galeropsis* which, although gastromycetoid, appears to have characters common to both families.

The following points must be considered before Van Overeen's concepts are accepted; the problem is best clarified by considering each subgenus in turn:

a) *Pholiotoideae: Pholiota, Kuehneromyces, Pachylepyrium, Pleuroflammula*

(1) BASIDIUM: The morphology of the basidia of members of the *Strophariaceae* does not agree with that of basidia typical of the *Bolbitiaceae*, i.e. short and broad. However, there are certain *Agrocybe* species whose basidia are slightly larger than predicted, a fact probably correlated with the thickness of the carpophore gill.

(2) BASIDIOSPORES: The basidiospores of *Pholiota* under the microscope are smooth, not very thick-walled, honey to yellowish brown in ammoniacal solutions and ellipsoid or slightly phaseoliform with a narrow often indistinct germ-pore. *Kuehneromyces*, however, has usually small, smooth basidiospores with a distinct germ-pore and fairly thick wall. *Pachylepyrium* was separated in part from the last genus by the very strongly pigmented, very thick-walled porate basidiospores; *Pleuroflammula* has similar thick and pigmented spores.

Whereas basidiospores of members of the *Bolbitiaceae* undergo a darkening to various degrees with alkali, no similar change is recorded in members of the above genera; such darkening has not been observed by me in *Pholiota* or *Kuehneromyces mutabilis*. The shape, thickness of spore wall, presence or absence of germ-pore must be considered in the light of correlated characters, for several members of the *Bolbitiaceae* have thick-walled spores, e.g. *Bolbitius vitellinus*, whereas others have very thin-walled spores, e.g. *Conocybe spiculoides*, and some aporate spores, e.g. *Agrocybe erebia* and *C. vestita*. In general, however, the spores of bolbitiaceous agarics although biparietal are simple, the inner wall being hardly discernible even with electron microscopic techniques. The spores of this family are generally fairly to distinctly broadly porate.

(3) COLOUR OF THE SPORE-PRINT: Spore-print of the *Pholiotoideae* is cinnamon brown or rusty fuscous or deep rust cinnamon (Ridgway: Army—Natal Brown, Walnut—Rood's Brown) and never approaches the richness of colour of spore-prints of *Conocybe* and *Bolbitius*. However, *Agrocybe* species have spore-print colours which approach very closely those mentioned above but lack both the cinnamon flush and the russet tinge of *Pholiota*.

(4) CYSTIDIA: Chrysocystidia are absent in the *Bolbitiaceae* but typify the genus *Pholiota* (excepting subgenus *Hemipholiota*). *Kuehneromyces* and the other two members of the *Pholiotoideae* lack pleurocystidia and chrysocystidia. In the first genus two types of cheilocystidia are frequently present. Cheilocystidia are always present in the *Pholiotoideae* although never of the rather symmetrical shapes found in the genera *Conocybe* and *Bolbitius*. Variability in cheilocystidial shape is more widespread in *Agrocybe* but here pleurocystidia are more typically found, often in considerable numbers.

(5) PILEUS CHARACTERS: The pileus in *Pholiota* subgen. *Hemipholiota* and *Eupholiota* is squamulose or scaly, a character not found in members of the *Bolbitiaceae*, even though at some stages of development cracking of the pileus produces a chequered aspect on the pileus in certain *Agrocybe* species e.g. *A. dura*. In the naked, dry or viscid *Pholiota* species chrysocystidia are present. *Agrocybe*, but for a few species, is typically hygrophanous or expallent, *Pholiota* is non-hygrophanous. The pileus characters of members of the genera *Kuehneromyces* and *Pachylepyrium* resemble more closely the pileus characters of *Agrocybe—Conocybe* in being hygrophanous and moist.

(6) HABIT/HABITAT: *Pleuroflammula* is pleurotoid, lignicolous and thermophilous. The other members of the *Pholiotoideae* are more typically lignicolous than bolbitiaceous agarics—*A. cylindracea* is an exception.

(b) *Strophariоideae: Stropharia, Hypholoma* (=*Naematoloma*), *Psilocybe* (including *Deconica*), *Melanotus*.

(1) BASIDIUM: See a) 1.

(2) BASIDIOSPORES: The basidiospores of all members of the genera *Stropharia* and *Hypholoma* are lilaceous fuscous, olive lilaceous or purple sepia under the microscope. They are always fairly constantly ellipsoid in shape, and in their double walled structure; they do not darken in alkali; are most often truncate and typically distinctly porate. In nearly all these respects, apart from colour, they parallel the *Bolbitiaceae*. In one group of agarics placed in *Psilocybe* the spores are typically lentiform. However, this character is also paralleled in the *Bolbitiaceae* in *Conocybe*, e.g. *C. antipus* and *C. hexagonosporus*.

(3) COLOUR OF SPORE-PRINT: No species attributable to the family *Bolbitiaceae*, as currently defined, has a spore-print with a colour approaching that found in the *Strophariоideae* (Ridgway: Bone Brown—Seal Brown).

(4) CYSTIDIA: *Stropharia* and *Hypholoma* are typified by the presence of chrysocystidia, structures unknown in the *Bolbitiaceae*. In *Melanotus* pleurocystidia are lacking and, in the genus *Psilocybe*, they are either present or absent. Cheilocystidia are present in all the groups; they are never lecythiform.

(5) PILEUS CHARACTERS: The pileus in the *Strophariоideae* is usually moist or viscid, frequently ornamented with remnants of a veil attached here and there. The pileus is never scaly and is typically non- or only slightly hygrophanous, often brightly coloured red, yellow, orange, tawny, green, etc., and thick fleshed. Bright colours in the *Bolbitiaceae* are rare and only found in *Bolbitius*.

(6) STIPE CHARACTERS: In the *Strophariоideae* the stipe is generally fibrillose-silky, tough, fleshy or fibrous and not fragile as in *Conocybe*; it is annulate or not and often viscid, with remains of veil.

(7) HABIT/HABITAT: *Melanotus* is usually thermophilous and pleurotoid and grows on decaying, not decayed, plant debris. *Stropharia* is frequently coprophilous and *Hypholoma* is typically lignicolous, much more so than *Agrocybe; Psilocybe* species are coprophilous or grow on base rich or

manured soil. Thus the habitat of many members of this subgenus are similar but careful analysis of the commonest species indicates that the majority of the *Strophariodeae* are "calcifuges". pH readings of the dung, wood and plant debris on which the carpophores of several members of the *Strophariodeae* grow are always acid and but for *Psilocybe semilanceata* often extremely acid: pH 4·0–3·5 (average 5·3 for sixty-five readings, infrequently greater than pH 5·8).

(8) BIOCHEMISTRY: Psilocybin and psilocin have been isolated from some *Psilocybe* species and, more recently, *Conocybe cyanopus* has been shown to contain the former compound (Benedict *et al.*, 1962). A second species of the genus *Conocybe*, *C. siligneoides* and certain *Stropharia* species are also recorded as being used as hallucinogenic principles and may indicate the presence of similar or closely related compounds in other members of the *Bolbitiaceae* (Heim, 1957; Wasson, 1961 and 1962).

(9) DEVELOPMENT: The paravelangiocarpic type of development is typical of the *Bolbitiaceae* and has been recorded in modified form for *Naematoloma polytrichi* (= *Hypholoma*) (Reijnders 1963). The *Strophariaceae* on the other hand, from the limited number of species examined, are typically bivelangiocarpic.

CONCLUSION: The distinctive development correlated with the presence of chrysocystidia and a epicutis composed of repent hyphae separates the *Strophariaceae* from *Agrocybe*. Nevertheless there is some connection between the families described above, particularly between *Agrocybe*, *Conocybe* and the *Strophariodeae*.

iv) **Hebeloma** (Fr.) Kummer, 1871.

Although Romagnesi (1962) suggested an affinity between *Agrocybe* and *Simocybe*, he had earlier (1937) placed the former genus close to *Hebeloma* in the *Phaeotaceae*. Again some resemblance in gross morphology, between members of the two genera may be considered, particularly *Agrocybe* and *Hebeloma* sect. *Hebeloma*, e.g. *H. mesophaeum*. This, however, is even less impressive than the resemblances already discussed under *Strophariaceae*. Many *Hebeloma* species do in fact resemble those of *Agrocybe* in their overall coloration, particularly of the lamellae and stipe and in the slightly greasy or faintly viscid nature of the pileus surface. The differences may be summarised as follows:-

(1) BASIDIA: *Hebeloma* species have basidia which are not typically short and broad.

(2) BASIDIOSPORES: Typically punctate rough basidiospores are found in *Hebeloma*, and they are frequently subacuminate at both ends and instead of a germ-pore there is a callus. The colour of the spore-mass is much more Snuff Brown (Ridgway).

(3) CYSTIDIA: Many *Agrocybe* species possess pleurocystidia although they are absent in other members of the *Bolbitiaceae*. *Hebeloma* resembles *Conocybe* in the fact that it lacks pleurocystidia.

(4) PILEUS "CUTICLE": In *Hebeloma* the outer layer of the pileus consists of filamentous hyphae encrusted with brownish material.

(5) SMELL AND TASTE: Most *Hebeloma* species have a characteristic odour, often aromatic or radishy. Apart from the mealy smell of *Agrocybe* species, distinctive smells or tastes are rare in bolbitiaceous agarics.

(6) DEVELOPMENT: In *Hebeloma* the development is monovelangiocarpic, not paravelangiocarpic as in members of the *Bolbitiaceae*.

(7) HABITAT: Most Hebelomas are silvicolous and more often than not connected with particular tree species—perhaps mycorrhizal (always?). Although species of *Conocybe* and *Agrocybe* often have special ecological niches they do not seem to be confined to certain tree species or groups of tree species.

It is of interest to note that probably J. Lange described an *Agrocybe* species in *Hebeloma* as *H. elatum* var. (?). He mentioned that the fungus which he named *H. elatum* resembled a large *Naucoria* (in the view of Lange this genus included many species of *Agrocybe*). Lange's drawings of the carpophore and basidiospores leave little doubt in my mind he was examining an *Agrocybe*.

The author feels that *Hebeloma* is probably more closely related to *Inocybe* and has no affinities with *Agrocybe*, nor therefore with the *Bolbitiaceae*.

v) **Coprinaceae** subfam. **Coprinoideae.**

Although some *Coprinus* species have basidia which in shape are short and broad there does not appear to be a very close connection between the *Coprinaceae* subfam. *Coprinoideae* and the *Bolbitiaceae* (see *Panaeolus* discussion). The deliquescence in *Bolbitius* is a post-mortem change after spore discharge and does not assist in the spore dispersal mechanics as it does in *Coprinus*.

The basidia in *Coprinus* are often trimorphic or dimorphic, a character in coloured-spored agarics unknown outside the *Coprinoideae*. Although *Coprinus* (and *Psathyrella*) possess a "cellular" cuticle they frequently exhibit a very distinct covering veil which may either consist of filamentous cells, spherical cells or mixtures of differently shaped cells. The gills of *Coprinus* are parallel or subparallel and not wedge-shaped as in the *Bolbitiaceae;* the shape of the gills in *Coprinus* is connected with the character of autodigestion.

The basidiospore colour is destroyed by concentrated sulphuric acid in members of the genera *Coprinus* and *Psathyrella* whereas no such reaction is noted in the *Bolbitiaceae* or *Panaeoloideae*. Coprinaceous spores show no colour change with alkali treatment.

The development of all *Coprinus* and *Psathyrella* species has been found to be bi- or monovelangiocarpic, usually the former. One agaric placed in *Psathyrella* subgen. *Conocybella* (Singer, 1948) has lecythiform cystidia but the author believes this is incidental and there is very little connection between the *Coprinoideae* and the *Bolbitiaceae* (but see discussion on *Panaeoloideae*).

vi) **Galerina** Earle 1909 and **Galera** (Fr.) Kummer 1871 non Blume 1825.

One of the oldest connections between a member of the *Bolbitiaceae* and another agaric family is *Conocybe* and *Galerina* (*Cortinariaceae*)*;* these genera appear in early works under the single generic heading *Galera*. The resemblance, however, is really quite superficial. The cuticle in *Galerina* is always filamentous and, therefore, when the pileus dries out it tends to give a rather different appearance to that of a *Conocybe* under similar conditions. The pileus of members of the latter genus glisten when dry whereas those of *Galerina* are quite mat.

The development of *Galerina* is typically monovelangiocarpic not paravelangiocarpic. Veil remnants are found more frequently in *Galerina* than *Conocybe*, they are cortinate and when remnants are present in members of the latter genus they are less filamentous and filmy except perhaps in *Conocybe vestita*.

The basidiospores of *Galerina* are not usually darkened by treatment with alkali; there are exceptions however, e.g. *G. marginata* complex. The spores are also rarely smooth, usually punctate or verrucose with a distinct suprahilar plage. Perispores are found in some *Galerina* species, e.g. *G. calyptrospora*, but are unknown in members of the *Bolbitiaceae*. The germ-pore typifies *Conocybe* but in *Galerina* the germ-pore is replaced by a callus. The colour of the spore mass is very similar in both *Conocybe* and *Galerina* perhaps the latter have spore-prints of Mikado Brown or Sayal Brown (Ridgway), colours not found in the *Bolbitiaceae*. Cystidia are never lecythiform in *Galerina* although they may be tibiform and pleurocystidia are frequent; the latter are unknown in *Conocybe*.

The habitat is very distinctive for *Galerina:* mossy banks, moss covered rocks, bare soil with high raw humus content, peat, moss soaks and other acid environments. *Conocybe*, on the contrary, inhabits base rich areas, alkaline dung, mole-hills, etc. The optimum growth in culture for *Galerina* is achieved at lower pH than for *Conocybe* (pH 4·2 as opposed to pH 7·25).

The variation in the genus *Galera* (as tribe and later subgenus of *Agaricus*) was known to Fries himself; he recognised three groups two of which made up the greatest part of his tribe. The polygeneric nature of *Galera* has been discussed in the introduction. *Galerina* is not related to *Conocybe*.

KEYS TO THE FAMILIES AND GENERA KNOWN TO CONTAIN SPECIES WITH BROWN OR OCHRE SPORE-PRINTS

A note concerning the two keys included in this account is required. The first key is to those genera recognised by Singer (1962) which contain agarics possessing a coloured spore-print but whose spore-print is never salmon pink, black, green or purple. The key is an attempt to place the *Bolbitiaceae* alongside the other brown-spored agaric families (and genera) even though to some they may be quite unrelated and only superficially similar. In no way have I altered Singer's concept of generic delimitation, not even that of the genera in the *Bolbitiaceae* which has been the focus of attention in the present paper; my present concepts are placed in brackets. In three important cases, which are indicated below, the concepts of Dennis, Hora & Orton (1960) differ markedly from Singer.

The second key is to those genera of British species which would have been placed in the *Ochrosporae* by Massee, W. G. Smith and others, or considered related in some way or confused with this group.

Nomenclature of genera has been based on Donk (1962) and nomenclature of specific names on Dennis, Hora & Orton (1960), except where personal research has indicated otherwise.

WORLD-WIDE KEY

1a. Trama heteromerous . . . . *Russulaceae*

1b. Trama homoiomerous 2

2a. Trama bilateral 3

2b. Trama not bilateral; spores* dextrinoid when the epicuticular elements are dextrinoid or amyloid (fide Singer) 4

3a. Hymenophore lamellate, decurrent, easily separable from the pileus tissue; clamp-connections ± present . . . . *Paxillaceae*

Long filamentous, brown conducting elements with sieve-like surface and sponge-like contents (coscinoids) present; spores verrucose to rough . . . *Linderomyces* Singer (1947) Coscinoids absent; spores smooth . . . *Paxillus* Fr. (1835). Spores echinate . . . *Neopaxillus* Singer (1948). (*Rhodocybe* Maire (1926) differs in the pinkish grey or buff spore-print).

3b. Hymenophore poroid or subporoid, easily separable from the pileus flesh (context); clamps always absent or ± present *Boletaceae* (*Xerocomoideae—Phylloporus* Quélet, 1888)

4a. Spore-print cream, pinkish buff, or very pale brownish pink. Spores microscopically subhyaline to hyaline . . *Tricholomataceae* (e.g. *Macrocystidia* Joss., 1934, *Ripartites* P. Karst., 1879 etc.—see Key to the genera occurring in Britain).

4b. Spore-print distinctly brown, some shade of ochraceous rust, red-brown, clay brown or snuff brown 5

5a. Extremely large lanceolate pleuro- and cheilo-cystidia present; spores under the microscope only very faintly coloured *Macrocystidia* Joss. (see step 4)

5b. Lacking gigantic cystidial elements or if large cystidia present spores under the microscope distinctly coloured 6

6a. Epicutis of pileus to some extent hymeniform or with a distinct, easily lost, epithelium 7

6b. Epicutis not so composed, lacking hymeniform structure or epithelium at all stages 9

7a. Epicutis of pileus strictly hymeniform or with a distinct detersile epithelium. Scalp of pileus "cuticle" always "cellular" . . 8

7b. Epicutis not a distinct and persistent hymeniform layer, often with mixtures of barrel-shaped cells filaments and elliptic elongate cells *Cortinariaceae* (*Inocybeae*)

Mycorrhizal, exosporial ornamentation present . . . *Alnicola* Kühner, 1926. Non-mycorrhizal, spore lacking ornamentation . . . *Simocybe* P. Karst., 1879 (Both genera together=*Naucoria* (Fr.) Kummer sensu Dennis, Hora & Orton, 1960).

8a. Epicutis strictly hymeniform, less frequently with a few accompanying epicuticular hyphae, true hairs ± present . . . *Bolbitiaceae*

Snuff brown spore-print . . . *Agrocybe* Fayod (1889). Rust spore-print; hymenophoral trama regular; coprinoid agarics; pileus viscid, plicate-sulcate . . . *Bolbitius*. Collybioid-mycenoid agarics, dermatocystidia ± present . . . *Pholiotina* Fayod (1889). Rust spore-print; hymenophoral trama reduced. Pileus plicate-striate . . *Galerella* Earle (1909). Mycenoid-collybioid agarics usually lacking dermatocystidia . . . *Conocybe* Fayod (1889) (the last three genera are all considered to belong to *Conocybe*).

* In this key the term *spore* will apply to the basidiospore.

8b. Distinct epithelium present . . . . . . *Agaricaceae* (*Cystodermateae; Phaeolepiota* Maire ex K. & M., 1928)

9a. Spores strongly echinate as in *Laccaria* (see *Cortinariaceae, Inocybeae: Inocybe*)

9b. Spores never so ornamented 10

10a. Spores not completely smooth, punctate or verrucose . . 11

10b. Spores smooth or nodulose or stellate, never punctate or verrucose 13

11a. Spore-print distinctly rust or rich ochre yellow, spores thick or fairly thick-walled with perisporial or exosporial ornamentation *Cortinariaceae* (*Cortinarieae*)

Non-mycorrhizal. Stipe central; spores smooth to coarsely verrucose with suprahilar plage . . . *Galerina* Earle (1909). With ornamented spores lacking plage and with tough cartilaginous rooting stipe . . . *Phaeocollybia* Heim (1931). Ornamented spores without plage and with fleshy thick stipe and bright yellow or golden gills . . . *Gymnopilus* P. Karst (1879) Stipe lateral . . . *Pyrrhoglossum* Singer (1944).

Mycorrhizal. Inner veil a cortina and outer veil fibrillose, scaly, glutinous or absent . . . *Cortinarius* Fr. (1836) (*Leucocortinarius* (J. Lange) ex Singer, 1945 differs only in the white spore-print). Double veil, inner one membranous, rust coloured spore-print . . . *Rozites* P. Karst. (1879). Simple veil and ochraceous yellow spore-print . . . *Descolea* Singer (1950).

11b. Spore-print distinctly clay brown, snuff or argillaceous . . 12

12a. Tricholomoid, collybioid agarics with sterile gill-margin and slightly or fairly thick-walled spores with ± distinct exosporial ornamentation *Cortinariaceae* (*Inocybeae: Hebeloma* (Fr.) Kummer: 1871)

12b. Clitocyboid, omphalinoid, mycenoid less commonly collybioid or pleurotoid agarics with thin and simple walled spores with ornamentation episporial or partially immersed in the episporium *Crepidotaceae*

Clitocyboid, mycenoid, or omphalinoid agarics, spores smooth to distinctly punctate . . . *Tubaria* (W. G. Smith) Gill. (1876). Pleurotoid agarics, spores smooth to distinctly punctate . . . *Crepidotus* (Fr.) Kummer (1871). Reduced cyphelloid forms . . . *Episphaeria* Donk (cf. also *Phaeosolenia* Speg. which is close to *Deconica* (W. G. Smith) P. Karst., 1879, fide Donk).

13a. Thick-walled cystidia encrusted with crystals (metuloids) present, spore print argillaceous brown . . . . *Cortinariaceae* (*Inocybeae: Inocybe* (Fr.) Fr., 1863)

13b. Metuloids absent 14

14a. Epicutis composed of repent hyphae with scattered dermatocystidia 16

14b. Epicutis composed of elongate broad, frequently incrusted, erect, hyphae and then with rust spore-print, or if subhymeniform with dermatocystidia then with argillaceous spore-print or "cuticle" composed of repent hyphae ± accompanied by dermatocystidia and with argillaceous spore-print . . . . . . (*Cortinariaceae*) 15

15a. Epicutis composed of elongate broad erect hyphae most frequently thick-walled and/or incrusted and with spore-print rust-brown (*Phaeomarasmoideae: Phaeomarasmius*† Scherfl., 1897, sensu Singer)

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† *Phaeomarasmius* sensu Singer, 1951 = *Phaeomarasmius* Scherfl., 1897 sensu Orton, 1960 plus *Flocculina* Orton, 1960.

15b. Epicutis subhymeniform or composed of repent hyphae ± with dermatocystidia and with spore-print argillaceous . (*Inocybeae*)

Probably always? mycorrhizal. . . . *Inocybe* (Fr.) Fr. Non-mycorrhizal; spores never stellate or nodulose; carpophores frequently with olivaceous tints . . . *Simocybe* P. Karst.

16a. Spore-wall easily collapsing . . . . . *Crepidotaceae*

Clitocyboid, omphalinoid, mycenoid or collybioid agarics . . . *Tubaria* (W. G. Smith) Gill. Pleurotoid . . . *Crepidotus* (Fr.) Kummer.* Cyphelloid genera related to the last—see step 12.

16b. Spore-wall thick to fairly thick-walled, not easily collapsing on dessiccation 17

17a. Habit typically agaricoid or secotiaceous 18

17b. Habit either pleurotoid or cyphelloid 20

18a. Spore-print not readily formed even under the most favourable conditions; pileus adhering to the stipe and only when fully mature exposing parts of the gill-system. Bolbitiaceous affinity *Galeropsis* Vel., 1930

18b. Normal spore-print formed with ease under favourable conditions; pileus expanding to expose gills 19

19a. Large or medium sized fleshy fungi often scaly or scurfy mostly lignicolous, saprophytic or parasitic . *Strophariaceae* (*Pholiotoideae*)

Spores complex and thick-walled, bright and strongly coloured brown even under the microscope . . . *Pachlepyrium* Singer (1958). Spores honey brown under the microscope and less complex; stipe central; pileus scaly or chrysocystidia present or related pleurocystidial types present . . . *Pholiota* (Fr.) Kummer (1871). Pileus not scaly, pleurocystidia rare or, if present, hyaline even after treatment with KOH . . . *Kuehneromyces* Singer & Smith (1946). Stipe eccentric . . . *Pleuroflammula* Singer apud Singer & Smith (1946).

19b. Small, membranous, collybioid, mycenoid or omphalinoid agarics, not scaly and mostly growing amongst moss or on bare soil particularly substrates of high organic matter content *Cortinariaceae* (*Cortinarieae*)

Spores ornamented and with supra-hilar plage . . . *Galerina* Earle (1909). Spores ornamented but lacking plage . . . *Phaeocollybia* Heim (1931).

20a. Cyphelloid . . . . *Crepidotaceae*
Reduced forms . . . *Pellidiscus* Donk (1959) (see also *Chromocyphella* de Toni & Levi, close to geophiloid agaric groups, fide Donk).

20b. Pleurotoid 21

21a. Rust brown spore-print . . *Strophariaceae* (*Pholiotoideae: Pleuroflammula* Singer)

21b. Snuff brown spore-print . . . . . . *Crepidotaceae: Crepidotus* (Fr.) Kummer (*Pleurotellus* Fayod, 1889, sensu Singer, 1951 non K. & M., Dennis, Hora & Orton, 1960; differs in the cream buff spore-print)

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* See Donk (1963) who quoted the authorities as (Fr.) Staud: 1857.

KEY TO THE GENERA OCCURRING IN THE BRITISH ISLES

1a. Carpophores with spongy flesh containing sphaerocysts. Spores* with amyloid ornamentation . . . . . 2 (*Russulaceae*)

1b. Carpophore lacking such structures in the flesh (context) . . 3

2a. Exuding colourless, white or coloured latex
Lactarius Pers. per S. F. Gray (1821)

2b. Not exuding latex, gills usually very brittle
Russula Pers. per S. F. Gray (1821)

3a. Spore-mass cream or buff, often with pinkish flush (resembling the various shades of face powder) 4

3b. Spore-mass not as above 12

4a. Smell of rotting fish or resembling cucumber. Cheilocystidia and pleurocystidia present, large and lanceolate. Pileus small—medium, light brown, dark brown to almost black, stipe similarly coloured, velvety
Macrocystidia cucumis (Pers. per Fr.) Heim ex Joss.

4b. Smell not as above 5

5a. Stipe lateral, absent or excentric
Crepidotus see step 15 (cf. also *Phaeomarasmius* step 16)

5b. Stipe not as above 6

6a. Spores warty-rough 7

6b. Spores not so ornamented 8

7a. Spores with amyloid ornamentation. Pleurocystidia when present often large, frequently barbed and often pointed. Carpophores medium to large; gills adnate emarginate . . *Melanoleuca* Pat. (1897)

7b. Spores lacking amyloid ornamentation. Cystidia absent. Carpophores medium to small; gills decurrent . . *Rhodocybe* (Maire 1926)

8a. Carpophore with distinct ring, volva or other form of veil . . 9

8b. Carpophore without evidence of veil 11

9a. Spores distinctly pigmented, spore-print pink or vinaceous brown, pileus cuticle "cellular", pleurocystidia present with crystalline excrescence. Growing either on wood or close to wood, often tufted
Psathyrella subgenus *Homophron* e.g. *P. sarcocephala* (Fr. ex Fr.) Singer

9b. Spores hyaline under the microscope, spore-print never as strongly pigmented; lacking ornamented pleurocystidia; pileus cuticle filamentous. Never lignicolous 10

10a. Carpophore exuding drops under moist conditions which later become rust or orange; stipe with peronate rings; spores small, rarely greater than 5 × 3μ; cheilo- and pleuro-cystidia clavate-fusiform or lageniform
Chamaemyces fracidus (Fr.) Donk

10b. Large carpophores not becoming rusty, with white, free gills; distinct volva and ring and often separable scales on the pileus
Amanita (*Aspidella* Gilbert) e.g. *A. echinocephala* (Vitt.) Quélet

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* In this key the term *spore* refers to the basidiospore.

11a. Medium to large carpophores with smooth, small spores less than 7·5μ in length and whitish cream, adnate gills which become spotted with red brown, rust or ochre . . . *Collybia* sect. *Striipedes*, e.g. *C. maculata* (A. & S. per Fr.) Kummer and *C. prolixa* (Hornemann per Fr.) Gillet sensu Moser

11b. Medium, large or small carpophores with decurrent gills and small spores but typified by the absence of cystidia and carpophore white, dull grey or brown or with faint russet flush . . *Clitocybe* spp. particularly *C. nebularis* (Batsch per Fr.) Kummer group. *C. fragrans* (Sow ex Fr.) Kummer & *C. phyllophila* (Fr.) Kummer

12a. Spore-mass brown but with distinct chocolate or purple tint when fresh 13

12b. Spore-mass lacking purple or chocolate flush to colour of spore-print 14

13a. Carpophores rapidly deliquescent, fragile or becoming papery, with or without veil; aequi-hymeniferous; basidia di- or trimorphic *Coprinus*

13b. Pileus with cellular "cuticle", not deliquescent, with or without veil but the latter rarely composed of sphaerocysts; inaequi-hymeniferous; basidia monomorphous . . . . *Psathyrella* spp. particularly those of subgenus *Hypholoma*, e.g. *P. candolleana* (Fr.) Maire and *P. hydrophila* (Bull. per Merat) Maire (note also *P. sarcocephala* step 9)

14a. Stipe absent or distinctly lateral and then usually very short 15

14b. Stipe neither lateral nor absent 17

15a. Spores smooth, warty or spiny less than 10μ in length, snuff brown in mass; gills not bruising reddish brown; carpophore small—medium usually the former, rather thin and often fragile *Crepidotus* (Fr.) Kummer (1871)

15b. Spores either greater than 10μ in length and rust in mass or spores smaller and then gills bruising red brown; carpophores tough or fleshy 16

16a. Spores greater than 10μ in length, rust or clay rust in mass; carpophores small or minute but nevertheless tough and pliable and reviving with water after desiccation *Phaeomarasmius* Scherfl. 1897 sensu Dennis, Hora & Orton

16b. Spores less than 10μ in length, gills decurrent, easily separable from the pileus tissue and becoming reddish brown when bruised, medium or large . . . . . . *Paxillus* Fr. (1835) (*Tapinia* Gilbert)

17a. Spore-mass with faint flush of greenish ochre or olive brown . 18

17b. Spore-mass otherwise, ochraceous brown, rust, snuff or clay brown 19

18a. Pileus small to medium, dry, smooth or velvety, with olivaceous tint when moist, drying ± ochraceous; spores 10μ or less, phaseoliform or amygdaliform; growing on wood or close to woody debris *Simocybe* P. Karst. (1879)

18b. Not as above, carpophores with distinct veil; pileus greasy or viscid cf. members of geophiloid genera, e.g. *Hypholoma elongatum* (Pers. per Fr.) Ricken

19a. Gills thick, distant, anastomosing 20

19b. Gills not thick nor becoming pore-like 21

20a. Gills thick, distant, often anastomosing to form elongated pores, yellow becoming golden and reddish on handling; spores subfusiform and stipe often radicate . . . . *Phylloporus* Quélet (1888)*

20b. Gills thick, distant, not becoming poroid; spores with germ-pore, elliptic to elliptic-amygdaliform . . form-genus *Ptychella* (abnormal forms of members of the *Bolbitiaceae*)

21a. Gills bruising reddish or brownish or on handling, easily detachable from pileus tissue, decurrent; stipe slightly excentric to central, ± on wood and spores smooth, elliptic-fusoid . . *Paxillus* Fr.

21b. Not bruising red-brown and not easily detachable from the pileus tissue. 22

22a. Gills free or becoming free; pileus viscid, thin and soon decomposing, almost deliquescent. Growing on wood, soil or herbaceous debris *Bolbitius* Fr. (1838) (including *Pluteolus* Gillet)

22b. Gills rarely free and if so, pileus never viscid, thin and "deliquescent" 23

23a. Pileus cuticle "cellular" composed of ovate, elliptic or barrel-shaped cells or covered in floccose meal consisting of spherical, elliptic or ovate cells entirely or in part 24

23b. Pileus cuticle filamentous composed of cylindric hyphae and, if scaly, hyphae of scales cylindric or cuticle with mixture of elongate hyphae and subglobose cells 28

24a. Pileus cuticle smooth or pubescent, strictly "cellular" . . 25

24b. Pileus with distinct floccose veil, epicutis never hymeniform . 27

25a. Spore-mass rust ochraceous, elliptic or elliptic-amygdaliform, smooth, very rarely finely punctate, with ± distinct germ-pore *Conocybe* Fayod (1889)

25b. Spore-mass buff, snuff or cigar brown variously shaped, smooth or rough with ± distinct germ-pore 26

26a. Spores smooth, usually elliptic or elliptic-subamygdaliform and usually with distinct germ-pore; carpophores with distinct or fugacious ring or with ± ring-zone . . . . . *Agrocybe* Fayod (1889)

26b. Spores rough, limoniform or amygdaliform, without a visible germ-pore; stipe without membranous ring, although a ring-zone may be present . . . . (see *Naucoria*, step 45)

27a. Carpophores large with well-marked membranous ring, and floccose veil composed of spherical cells which covers the pileus and stipe below the ring; spores smooth or faintly rough, elliptic—subfusiform, without germ-pore, ochre in mass. Cheilo- and pleuro-cystidia absent *Phaeolepiota aurea* (Mattuschka per Fr.) Maire ex K. & M.

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* The fungus which stands foremost in the mind is *P. rhodoxanthus* (Schw.) Bres. As the author pointed out a second closely related species may also be present in the British Isles (Watling, 1963); Singer's (1945) notes are relevant here.

27b. Pileus covered with floccose veil when young, but which is not composed of spherical cells, more rarely fibrillose, floccose or squamulose; ring absent; spores smooth, elliptic, ochraceous or rust in mass without germ-pore . . . . . *Flocculina* Orton (1960)

28a. Spores clay ochraceous or snuff brown in mass, more or less subglobose, spinulose or warty, less than 5μ in diameter; pileus small to medium, whitish or clay coloured; gills ± decurrent; cheilocystidia absent . . . . . . *Ripartites* P. Karst. (1879)

28b. Spores not spinulose-warty 29

29a. Cuticle heterocellular with mixture of filaments, cylindric hyphae and globose cells . . . . . . (see *Naucoria*, step 45)

29b. Cuticle strictly filamentous, composed of repent hyphae . . . 30

30a. Large terrestrial species with well-developed membranous striate ring; pileus and stipe with a furfuraceous silky white veil which persists on the pileus; spores rough, amygdaliform, large 10–13μ long and rust in mass; cheilocystidia cylindric clavate
Rozites caperata (Pers. per Fr.) P. Karst.

30b. Spores and cheilocystidia different; if large agaric with membranous ring then the pileus viscid or carpophore lignicolous or cortina present as well as a ring 31

31a. Spore-mass ochraceous, rust or rust-brown 32

31b. Spore-mass clay, snuff, cigar or buff brown 39

32a. Small to large mycorrhizal fungi; stipe and pileus margin joined when young by a conspicuous cortina, which collapses on the stipe as a fibrillose ring-zone, in addition to the floccose, fibrillose, dry or viscid ring-zone or zones already present there. Pileus dry or viscid, hygrophanous, expallant or not, gills lacking conspicuous cystidia but often powdered rusty due to spores when mature *Cortinarius* Fr. (1836)

32b. Cortina or ring-zone, if present, then carpophore lignicolous; pleurocystidia present or absent 33

33a. Pileus distinctly scaly and not hygrophanous 34

33b. Pileus smooth or with faint whitish hoariness left from veil . . 35

34a. Reviving with water after drying, pileus and stipe small, dry and scaly, spores smooth, on twigs and woody debris
(see *Phaeomarasmius*, step 16)

34b. Not marasmioid in nature; pileus large, yellow, tawny or rust, rarely dark brown; stipe with or without scales below ring or ring-zone; chrysocystidia ± present; spores without germ-pore. Growing on stumps, logs and twigs, some species parasitic
Pholiota (Fr.) Kummer (1871)

35a. Pileus small to medium, conical or acutely or obtusely umbonate, often viscid, sometimes brightly coloured; stipe tough, cartilaginous, frequently rooting; spores rough, without supra-hilar plage and less than 10μ in length . . . . . *Phaeocollybia* Heim (1931)

35b. Neither tough nor cartilaginous and lacking rooting base to stipe 36

36a. Habit mycenoid infrequently bigger, with campanulate-convex pileus and slender stipe; pileus striate at first, rarely viscid with or without ring; carpophore generally ochraceous yellowish, tawny rust or honey coloured; spores punctate or rough, rarely smooth, or, carpophore much larger, caespitose, lignicolous, darker brown in colour and stipe with distinct ring . . . . . *Galerina* Earle (1909)*

or Pileus always large-medium, hygrophanous, dark yellow rust or tawny, paler when dry; stipe with distinct ring beneath which it is scaly, caespitose, lignicolous; spores always smooth . . . *Kuehneromyces mutabilis* (Schaeff. per Fr.) Singer & Smith (1946). Pileus hygrophanous, rarely ever exceeding 25 mm; carpophores exceptionally caespitose, rarely lignicolous and then mycelium never permeating the woody tissue; spores punctate or rough less frequently smooth and if smooth carpophore never lignicolous nor with distinct ring and scaly stipe . . . *Galerina* Earle (1909).

36b. Not as above, never mycenoid, pileus less frequently campanulate-convex or hygrophanous, lacking honey or tawny tints . . 37

37a. Pileus soon expanded, often pale in colour, ochraceous with pinkish buff flush sometimes rust tawny, when moist striate or not, sometimes ornamented with white or pallid veil fragments; gills decurrent, arcuate or triangular; spores pale in colour under the microscope, frequently thin-walled . . . *Tubaria* (W. G. Sm.) Gillet, 1876

37b. Spores thicker walled and more strongly coloured under the microscope; gills never decurrent nor arcuate 38

38a. Pileus viscid or dry, pale or less frequently strongly coloured, not striate at the margin; gills generally pallid, yellow or ochraceous buff rarely if ever deep rust; spores smooth
Pholiota sect. *Flammula* (= *Flammula* Fr. ex Fr. pro parte [Section *Udi*])

38b. Pileus never truly viscid, usually brightly coloured, smooth or minutely scurfy, rarely striate at edge; gills often bright yellow or golden rust or rust spotted; spores typically punctate or rough
Gymnopilus P. Karst. (1879)

39a. Carpophore large, frequently smelling of cherry laurel; stipe annulate often scaly below ring and with rooting base often attached to buried wood, old roots etc.; spores amygdaliform or limoniform, rough, up to 10μ long; pileus bright buff or paler with separable adpressed fibrils; cheilocystidia present
Hebeloma radicosum (Bull. per Fr.) Ricken (see step 45)

39b. Combination of characters otherwise 40

40b. Pileus small—medium, with viscid, separable pellicle, olivaceous or umber sometimes tinged tawny; stipe often long, with brownish olive floccose or squamulose veil, at least in middle part, or veil forming ring-zone . *Pholiota myosotis* (Fr. ex Fr.) Singer (see steps 37 and 41)

40a. Characters otherwise, lacking olivaceous tints to both pileus and stipe 41

41a. Terrestrial; mycorrhizal (always ?) 42

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* Dennis, Hora and Orton, 1960 place *Pholiota mutabilis* (Schaeff. ex Fr.) Kummer in *Galerina* considered by some (e.g. Singer (1962)) to be taxonomically and phylogenetically unjustified. It is considered that the inclusion of *Kuehneromyces* also in the key as an alternative is justified. In this paper I wish to make no further comment.

41b. Lignicolous occasionally parasitic never mycorrhizal, large agarics with annulate stipe and often scaly below the ring, pileus yellowish or umber with separable adpressed fibrillose scales, dry or viscid and with smooth spores . . *Pholiota* (=*Eu-pholiota* Lange, 1938)

42a. Spores nodulose or smooth, never roughened nor punctate between the protruberances of nodules, phaseoliform, elliptic or amygdaliform 43

42b. Spores rough, spiny or punctate 44

43a. Pileus silky smooth or commonly fibrillose-scaly, radially fibrillose or rimose, rarely slightly viscid; gills free, adnate or subdecurrent, sometimes emarginate, whitish or clay at first, then ± olivaceous or dirty brown, finely snuff or cigar brown; cheilocystidia always present ± facial cystidia and then often very thick-walled; spores nodulose (subgen. *Clypeus*) or smooth (subgen. *Inocybe*) *Inocybe* (Fr.) Fr. (1863)

43b. Pileus possibly scurfy but not silky smooth, radially fibrillose or rimose, never viscid; gills usually adnate, whitish or clay at first finally with olivaceous cast; cheilocystidia always present but never thick-walled; pleurocystidia always absent and spores always smooth. Carpophore ± distinctly olivaceous . . . . *Simocybe* (see step 18)

44a. Spores subglobose beset with blunt cylindrical processes up to 2μ long, with the general appearance of a naucorioid agaric, with conical, bay or chestnut, squamulose pileus; reddish buff coloured flesh; stipe ± bulbous; cystidia fusoid ventricose thick-walled
Inocybe calospora Quélet apud Bres. (1882)

44b. Spores lacking large processes and cystidia different, never thick-walled 45

45a. Carpophores mycenoid, never tricholomoid; pileus ochraceous, ochre buff or tan coloured, neither smelling of radish or aromatic substances, frequently acidulous, taste not radishy but often bitter; ring absent but ring-zone, from remains of fugacious veil, sometimes present. Growing in wet places, often under members of the *Salicales*
Naucoria (Fr.) Kummer (1871)

45b. Carpophores tricholomoid to collyboid, less frequently mycenoid; pileus whitish or pinkish, or reddish buff, sepia or vandyke, lacking scales at disc; stipe either with cortina or with floccose or fibrillose ring-zone or not, or cortinate and then pruinose or smooth. Often smelling and tasting radishy or with aromatic odour
Hebeloma (Fr.) Kummer (1871)

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