TRAVAUX MYCOLOGIQUES

dédiés à

R. KÜHNER

Numéro spécial du Bulletin de la Société Linnéenne de Lyon
43e année ——————————— Février 1974

DIMORPHISM IN *ENTOLOMA ABORTIVUM*[*]

by Roy WATLING

DEDICATION

The present contribution has been offered as a thanks to Professor R. KÜHNER for his services to world agaricology. Although not covering a European agaric the contribution takes its form from the merger of both experimental and classical taxonomic approaches. In this way a method of approach has been used which Professor KÜHNER has in his dedicated years in mycology been keenly active in encouraging.

Summary. — The agaric *Entoloma abortivum* has been analysed in pure culture commencing with tissue from carpophoroid and agaricoid fruit-bodies and from basidiospores of the latter. The carpophoroid is composed of mycelial elements from both *E. abortivum* and the agaric *Armillaria mellea*; the latter is lacking from the agaricoid fruit-body. It is suggested that the carpophoroids of *E. abortivum* are formed by the activity of *Armillaria mellea* disorganizing the mechanisms which control the smooth expansion of the pileus.

INTRODUCTION

Entoloma abortivum (Berkeley & Curtis) Donk, a fungus probably better known by the old name *Clitopilus abortivus,* is frequently noted in mycological discussion for its ability to produce two forms of fruit-body. The normal form in which the fruit-body occurs is agaricoid, with fully developed pileus, lamellae and stipe and a second form, called the carpophoroid, which often accompanies, dominates or sometimes replaces the agaricoid (Plate 3 A & B; plate 4 H). The latter form produces conspicuous masses of tissue which are sometimes spore-bearing and when apparently fully developed is typically subglobose. Such carpophoroids have sometimes been referred to as the gastroid or atavistic aberration of an otherwise gymnocarpic fungus.

---

[*] In part the subject of a paper delivered to the First International Mycological Congress, Exeter September 1971.

E. abortivum is found in North America and recorded from Florida, Louisiana, Maryland, Massachusetts, Michigan, Minnesota, New York, North Carolina, Rhode Is, Tennessee Vermonto Virginia and Nova Scotia Ontario Quebec [1]. The present study commenced with the examination of cultures from material collected on a study-tour in Eastern North America in 1969. The study-tour was financed in part by Grant GB - 6908 01534 from the National Science Foundation of America made available to me through the research programme of Professor A.H. SMITH, University of Michigan.

MATERIALS

Description of fresh specimens.

Pileus (12)-40-100-(170) mm broad, convex then expanded, plane to broadly umbonate, or slightly and broadly depressed, « drab » [2], light drab or pallid mouse-grey or pale olive buff, then uniform greyish to avellaneous, densely and usually radially fibrillose-pubescent or silky at times, becoming smooth, more or less zoned, not markedly expallent; margin at first frequently incurved becoming revolute later. *Stipe* 20-70-(120) mm / 6-12-(18) mm, concolorous with pileus or paler greyish, fibrillose or scurfy especially at the often slightly swollen apex, sometimes striate below from mycelial covering, equal or subbulbous, white, solid, with white mycelial tomentum at base. *Lamellae* short, decurrent to adnexed, pale greyish then pinkish, buff-pink, pinkish cinnamon or avellaneous, crowded, narrow to medium, broad, narrowed towards the margin, concolorous, with roughened or even margin. *Flesh* white in pileus, white or light drab in stipe; *odour* and *taste* farinaceous or becoming nauseous especially after mastication. *Spore-print* cinnamon or wood-buff.

Basidia 4-spored, 30-35 x 7-9 μ. *Basidiospores* 7-8-(10)/5-6 μ, 5-6 sided,

---

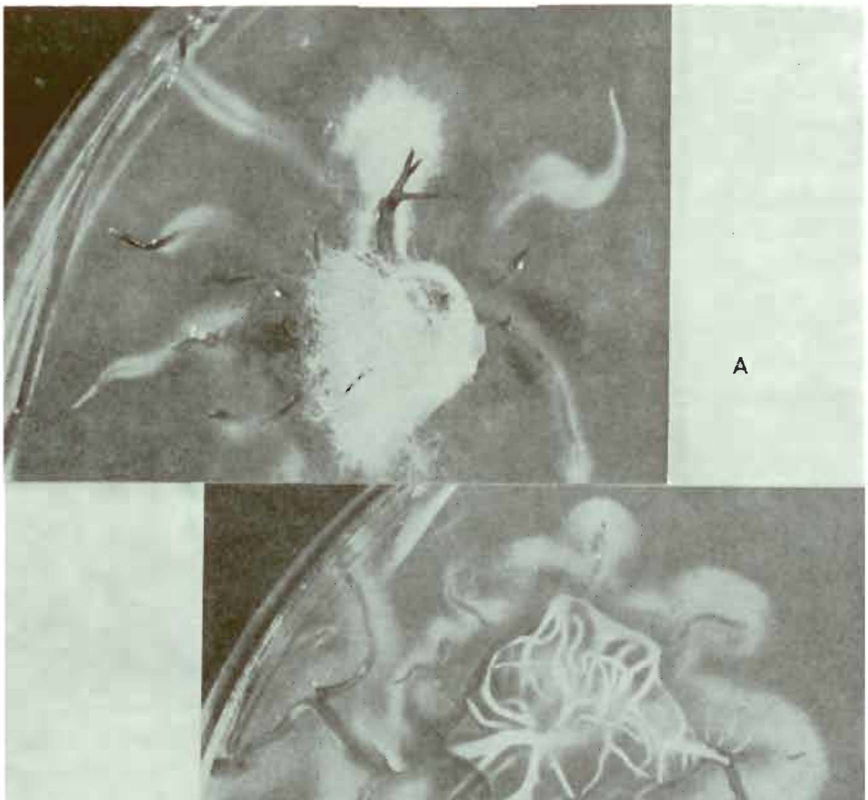
[1] MAZZO (pers. comm., 1973) informs me it is found in the Vera Cruz region of Mexico, and Japan.

[2] Colours follow : — Ridgway, R. (1912) Color standards and nomenclature, Balti-

---

Photograph.

Plate 1 A. Culture from carpophoroid of *Entoloma abortivum* showing rhizomorphs of *Armillaria mellea* and white mycelium of *Entoloma* segmenting out from the uppermost side; note the small white club-shaped structures on the rhizomorphs (Watling 6976) B. Reverse of A showing the unpigmented submerged rhizomorphs pushing the culture media up from the petri-dish surface in places; C. Herbarium material (Miller 9075) showing rhizomorphs attached to carpophoroids.


A
B
C

angles often rather sharp, honey-colour both in water and ammoniacal solutions, non-amyloid in Melzer's reagent. *Pleurocystidia* and *cheilocystidia* absent. *Hymenophoral trama* subparallel of hyphae 3-7 μ broad; *subhymenium* indistinct. *Pileipellis* of more or less erect filamentous hyphae. *Caulocystidia* of cylindric-clavate, terminal cells of hyphae in tufts or mounds. *Clamp-connections* present.

Caespitose to gregarious or often in troops. On soil, humus or decayed logs in deciduous woods.

Gastroid form.

Receptacle 10-75 mm, pyriform, ellipsoid, ovoid or subglobose, fleshy, white to dingy buff, broad above half-way, wrinkled to furrowed partilarly towards the base, irregularly pitted on sides or even extending on to upper surface. *Stipe* absent, reduced to a small mound of tissue or in ovoid fruit-bodies running into the pileus without distinction. *Flesh* white to dingy buff throughout, watery mottled, irregularly pitted in places, often friable in the median areas, flecked with red-brown harder areas particularly towards the base, discoloured pockets often developing with age. *Lamellae* absent or reduced to small pits which are lined with a palisade of cells resembling a hymenium. *Basidia* 4-spored. *Basidiospores* similar in all ways to agaricoid form, sparse. *Pleurocystidia* and *cheilocystidia* absent. *Hymenophoral trama* absent, (reduced or indistinguishable), or of irregular distribution. *Pileipellis* absent or considerably reduced. *Caulocystidia* not seen. *Clamp-connection* present.

In the vicinity or even attached to the normal fruit-body.

Material examined

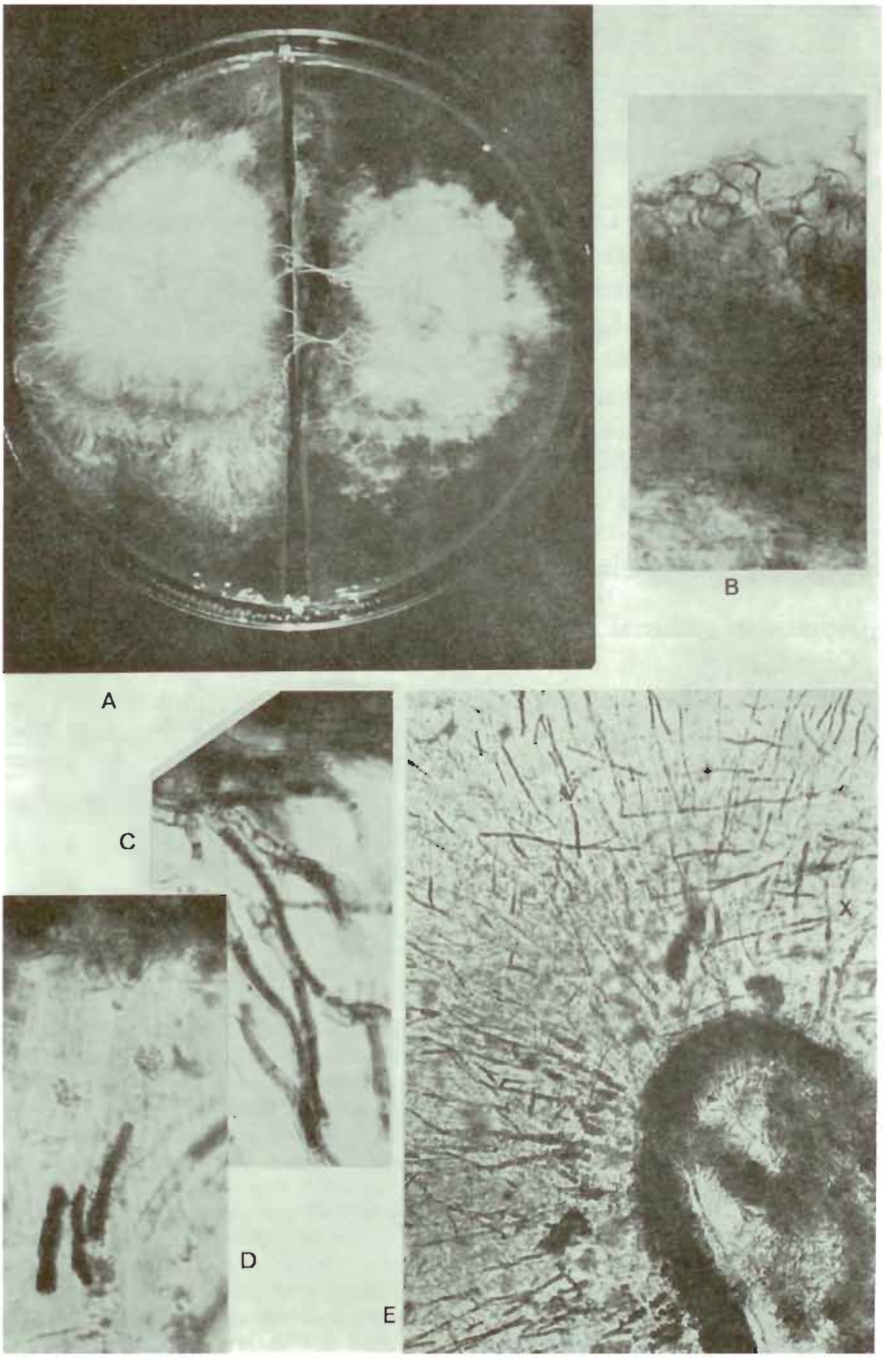
dagger denotes collections from which cultures have been obtained; asterisks denote the gastroid form is included in the collection, ** entirely aborted, * part of collection gastroid only.

United States

Florida: Seminola Co., August. 10th 1957. P.O. Schallert F 399 *

Massachusetts: Mount Toby, Sunderland, Franklin Co., legit Miss Jones Oct. 13th 1969. Watling 8013 *

Plate 2 A. Two isolates of *E. abortivum* surmounting the petri dish partition and freely anastomosing; B. Micrograph of rind cells of rhizomorph in TS; C. Micrograph of rind cells of rhizomorph in LS; D. Micrograph of hyphae from X in E. showing crystal depositis; E. TS of rhizomorph of *Armillaria* from culture of carpophoroid of *E. abortivum* showing radiating pattern of fringe hyphae with accompanying crystalline material, thick-walled almost opaque rind of rhizomorph and inner floccose zone. A. left Watling 6976; right Watling 6938. B.-E- Watling 6976.


B
A
C
X
D
E

Michigan: Waterloo Recreation area, Jackson Co., Sept. 4 th 1965. Wat. 1358 A/1658 C and 1385 A/1674 C (legit A.H. Smith) and Sept. 5 th 1965, A 1491/1764 C; George Reserve, Livingston Co., legit R. Homola, Sept. 4 th 1965, A 1481/1754 *; Sharon Hollow, Washtenaw Co., Mrs Florence Hoseney, Oct. 3 rd 1969, Wat. Nos. 6938, 6957 **, 6976, 6997 *, 6999 **

New York State: Greenbush ex coll. Charles H Peck, Albany, New York, in Herb. C. B. Plowright. *

North Carolina: near Highlands, Macon Co., Sept. 5 th 1939, Hesler 12327; Tennessee: Mr Le Conte, Sevier Co., Oct. 4 th 1936, Hesler 9510; Elizabethton, Carter Co., Aug. 28 th 1946, Hesler 17713.

Virginia: 30 miles north Danville, Pittsylvania Co., Sept. 24 th 1967. O.K. Miller 6125 *; Cascades Trail, Jefferson Nat. Pk., Culpeper Co., Sept. 28 th 1970, O.K. Miller 8743 * & Nov. 5 th 1971 O.K. Miller 9075 *.

All the collections are in (E) excepting the material from Virginia which is housed in the Miller Herbarium, Virginia Polytechnic Institute and State University, Blacksburg, Virginia.

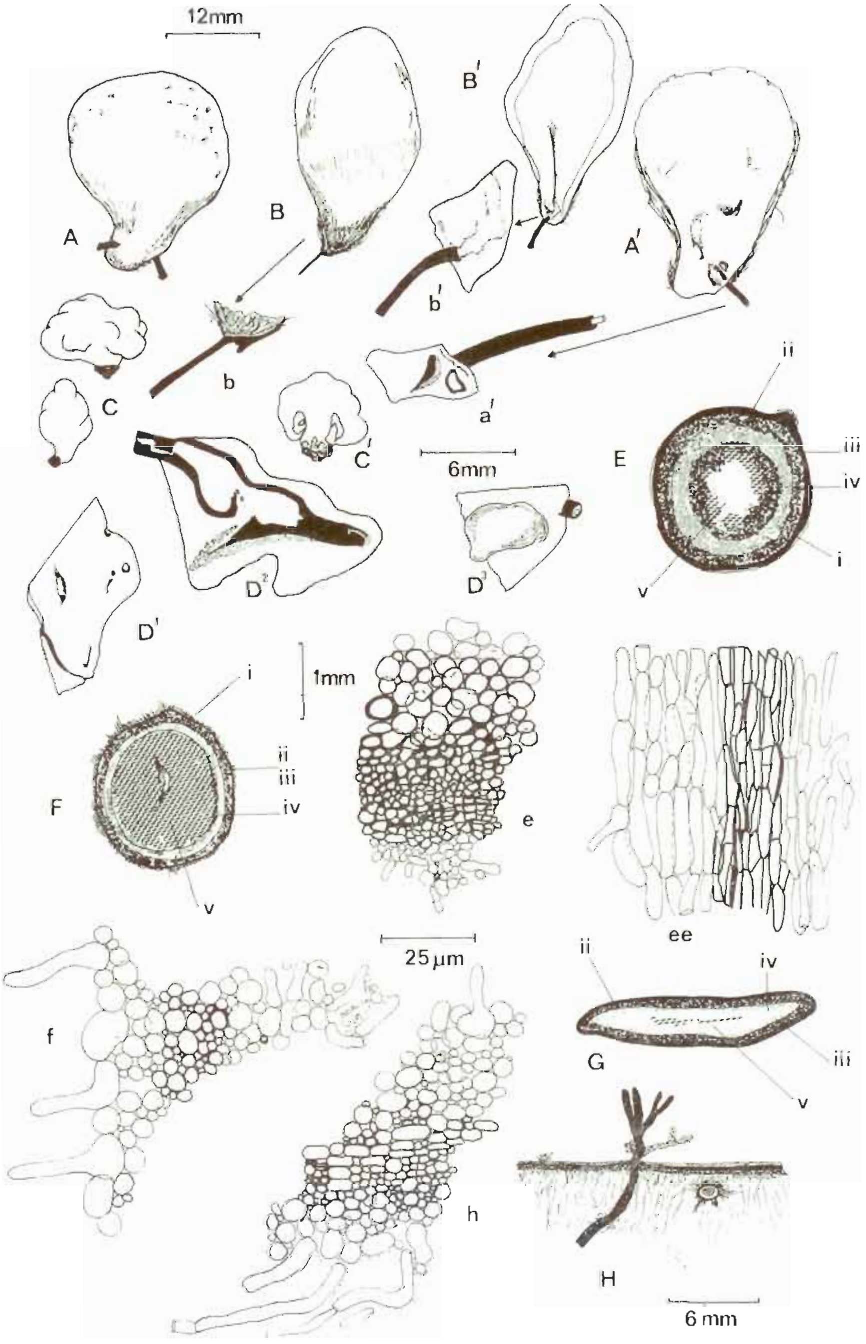
Additional material from K

Canada:

Ontario, London. Sept. 1914, J. Dearness - 2 collections as 4517 Fungi Columbiani - E. Bartholomew * (one collection IMI 28312) and United States Dept. Agriculture: Mycological Exchange 1126 (Dupl. F. Coll. 4517): Skyline Trail, Gatineau Park, coll. Conners, Sept. 7 th 1942 DAOM. 11970.

United States:

Plate 3. A and B. Carpophoroids of *Entoloma abortivum* and sections (A' & B') : detail of basal areas given in b, a' & b'. Watling 1358A/ 1674 C. C & C' Carpophoroids and section respectively of *Inocybe geophylla* var *lilacina* Watling 6582. D'-D^3 sections of basal areas of carpophoroids to show darkened hyphae of *Armillaria mellea* with in the *Entoloma* tissue. E. T.S. of fully pigmented rhizomorph from culture of Watling 6976 (i) outermost layer of collapsed and not strongly pigmented or thickened cells. (ii) zone ot thick walled strongly pigmented cells (iii) zone of fused thick-walled cels (iv) zone of thin-walled cells (v) central cavity with disorganising thin-walled cells; e, f ee, T.S. & L.S. SE magnified; F. T.S. of young pale-coloured rhizomorph : culture no. and labelling as in E; f.T.S. of F. magnified; G. flattened mature rhizomorph from old culture, culture no. and labeleling as in E; note absence of (i), H. L.S. of sclerotial plate showing two rhizomorphs one in T.S. and the other pushing through the sclerotial plate. Note hyphal tufts and the similarity of structures i-iv in E, F & G.; h, L.S. of sclerotial plate magnified. Magnifications as indicated E - H, Watling 6976. (E).


12mm
A
B
b
B'
b'
A'
a'
C
C'
D'
D²
D³
6mm
E
i
ii
iii
iv
v
1mm
F
i
ii
iii
iv
v
e
ee
25 µm
f
h
G
ii
iii
iv
v
H
6 mm

Michigan : South Lyons Smith 5046, Oct. 6 th 1936 ; Kellogg Forest, Kalamazoo Co., R. A. Shoemaker DAOM 51140 Sept. 1955.

Notes accompanying the type material of Berkeley (Sprague No 5737) leave no doubt that the fungus on the type folder at K is identical to material from which the cultures used in the present study were obtained.

C.J. Sprague states :

« a defined species in damp woods very gregarious. It is found in clumps of all ages connected by a thick, white, cottony mycelium and alternating with abortive growths. These are round, fleshy, juicy and depressed in the centre. They are covered with the same white, fleecy mat as the stipes of the perfect plants and lie among them ! »

SPRAGUE in fact illustrates in addition to a group of agarics and a section of a single agaric, a single aborted fruit-body.

Rvs. BERKELEY & CURTIS equate their fungus with *Agaricus popinalis* Fries (= *Rhodocybe* Maire) and mention the aborted state « often abortive and then presenting subglobose umbilicate downy masses ». This is taken by BERKELEY from Sprague's field-sketch which accompanies his material but as indicated by the present description the gastroid form is very much more variable.

Cultures.

Tissue-cultures were prepared on both Hagem's medium agar and 2 % malt-extract agar from both agaricoid and carpophoroid fruit-bodies. Tissue was isolated from what appeared to be a veil-like tissue from the pileus, from the stipe in the carpophoroid fruit-body and from the pileus and stipe in agaricoid fruit-bodies. Material was obtained from several individual collections from around Ann Arbor, Michigan and from Mount Toby, Massachusetts. Later cultures were obtained from O. K. MILLER who isolated the fungus from a carpophoroid fruit-body and the spore-print of a normal fruit-body both collected in Virginia [1].

In certain instances tissue from the « veil », pileus and stipe of the carpophoroid fruit-body produced cultures in which two separate types of mycelium segmented out, a white fluffy mycelium (termed type I) and a

---

[1] In preparing fresh cultures of material from Massachusetts Prof. H. BIGELOW in a letter dated 13-XI-1971 writes — « I guess that I had never cultured this species before, and was quite interested to note that the abnormal form produced rhizomorphs like. (*Armillaria*) *mellea* in a petri dish culture. » This confirms the information presented herein. Professor H. BIGELOW kindly sent cultures prepared from both aborted and normal fruit-bodies.

pinkish buff mycelium (termed type II) which produced darker hyphae below (Plate 1 A & B). When pure cultures of both these mycelia were obtained they remained vegetatively stable, the first producing white rhizoidal threads and greyish buff sclerotia whilst the second was more restricted in growth, producing pinkish hyphae with long, dark red-brown rhizomorphs. These latter structures were brown with long, dark red-brown rhizomorphs. These latter structures were brown with white tips and where they came to the surface of the agar they produced plates of red-brown sclerotial material and pinkish brown tufts of mycelium. The agaricoid form, on the other hand, produced white fluffy mycelium but never the dark rhizomorphs; the only differentiated structures formed were sclerotia. Similarly the culture produced from the basidiospores had only the white fluffy type of colony. Anastomosis between the white fluffy cultures from all the isolates analysed could be easily obtained (Plate 2 A) but no such anastomosis occurred between the first and second types of culture although some stimulation was seen.

Herbarium studies.

When dark mycelium had been isolated in culture from *Entoloma abortivum* all the herbarium collections available were examined to seen. Out of seventeen collections 50 % of those containing carpophoroid fruit-bodies had rhizomorph development, indeed in some collections the development was very evident. All the material sent to us from Virginia Polytechnic Institute and State University had showed rhizomorphs, which in two collections reached several centimetres in length (Plate 1 C). Several specimens were sectioned and the rhizomorph was seen to enter the base of the carphoroid and form a plate or fan of darkened hyphae. These darkened hyphae were connected to paler, thinwalled hyphae wich permeated the tissue in some carpophoroid fruit-bodies entirely, in others only in the basal region. When mycelial extensions of the rhizomorph were found in the tissue they were found usually to be associated with pockets or cavities where there was an apparent disorganisation of the tissue.

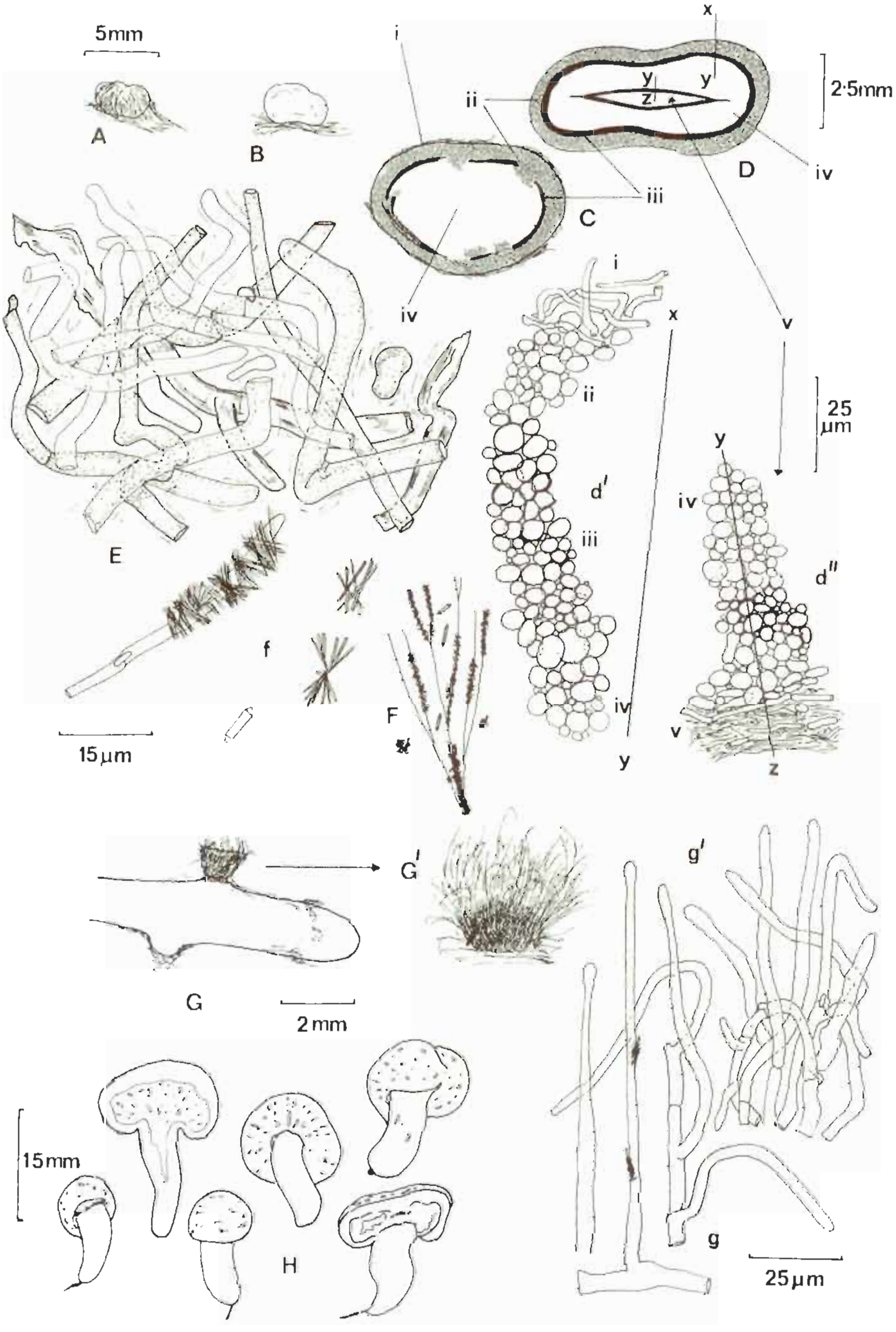
Sections of the herbarium material indicated that on certain gastroid fruit-bodies basidia were produced, often in the cavities of the pitted pileus-surface; in some cases basidiospores were produced and in no way differed in morphology from those produced by the agaricoid form. It has not yet been possible to test the germinability of these spores. Sections of the rhizomorphs indicate that they are similar in structure in all ways to those found in culture and only the matrix of the carpophoroid was found to resemble the colonies obtained from culturing the tissue of the agaricoid form.

IDENTIFICATION.

Rhizomorphs both of cultured and herbarium material resemble those of *Armillaria mellea* (Vahl ex Fr.) Kummer in gross morphology * and sections agreed in all major features with the diagrams prepared by TOWNSEND (1954) and with sections produced from material of British origin. The rhizomorph of *Armillaria mellea* is quite complex and its organization allows it to be picked easily out from a range of other superficially similar structures (Plate 3 E, F & H), eg., rhizomorphs produced by *Marasmius androsaceus* (Linn. ex Fr.) Fr., *Hysterangium nephriticum* Berk., *Tricholomopsis platyphylla* (Pers. ex Fr.) Singer, *Phallus impudicus* Linn. ex Pers. One further character of *Armillaria mellea* which sets this fungus aside from any other species producing highly organised rhizomorphs is its luminosity when observed in the dark. All the cultures of Type II viewed in the dark were luminescent and in this way differed from all cultures of Type I. Sections of sclerotial plates and associated structures showed extremely good correlation with *Rhizomorpha subterranea* Pers. and *R. subcorticalis* Pers. (plate-structure). Several different isolates of *Armillaria mellea* of British origin were compared with the isolates of Type II which they resembled closely in many ways. There were some minor differences but these were not any greater than the differences between the British isolates themselves used in the study, a perturbing variation noticed by many other workers. Gross differences in genotype of *Armillaria mellea* may be indicated in several ways, in differences in growth pattern, ability or difficulty in obtaining hyphal fusions etc. between different strains. Hyphal fusions were obtained between Type II cultures from Michigan material but not convincingly between Type II collections from different

---

Plate 4. A. Young sclerotium of *Entoloma abortivum* with covering of hyphae. B. mature glabrous sclerotium; C & D, sections of immature and mature sclerotia recpectively (i) outer loose covering of hyphae (ii) zone of rouded closely packed, thin-walled cells (iii) zone of pigmented, thick-walled cells (iv) inner zone of thin-walled cells wich at maturity may develop a central cavity (v) lined with a layer of pigmented hyphae; d' & d" section through D at xy and yz recpectively; E. loose, thin-walled, filamentous hyphae from (i); F. plan of vegetative hyphae of *Armillaria mellea* in culture showing crystals; f. one hyphae and crystals magnified. C. Rhizomorph of Watling 6976 wit'h hyphal tufts', G' individual 'tuft' magnified, g & g' cystidoid elements from the margin and central zone of the turf respectively. H. carpophoroids of *Entoloma abortivum* with section, Watling 1385 A/1674 C (E).


5mm
A
B
i
ii
iii
iv
C
x
y
y
z
2·5mm
D
iv
iii
E
i
ii
x
d'
iii
iv
y
v
25 µm
y
iv
d''
v
z
f
F
15 µm
G
G'
2 mm
g'
g
25 µm
15mm
H

states in the Union. The taxonomy of *Armillaria mellea* in the United States is in need of revision, indeed in the British Isles considerable variation in morphology of the fruit-body may be recorded. Rolf SINGER has been placed on record as saying the taxonomy of *Armillaria mellea* is almost a sub science in itself! (see Petersen 1971).

When aqueous suspensions containing macerated mycelium of Type I, i. e *E. abortivum,* and of British collections of *Armillaria mellea* are placed together on agar - surface, they show very rapid and active growth suggesting some type of mutual or unilateral stimulation is present, a stimulus also observed when Type I cultures from Michigan, Massachusetts and Virginia are grown in the present of control Type II cultures in a partitioned petri-dish. In all cases Type I cultures rapidly grow over the partition and into the Type II culture whose rhizomorphs branch freely through the dual system so formed.

STRUCTURE AND DEVELOPMENT OF SCLEROTIA

Two distinct structures were found in Type I isolates, thin, white, flexuous aggregates of hyphae (Plate 2 A) and hard olivaceous buff or sepia-brown sclerotia, which on washing were dark red-brown or umber (Plate 4 A & B). Sclerotia germinate immediately when placed on fresh agar by producing vegetative mycelium and if washed in 10 % aqueous solutions of furfuraldehyde; white fluffy mycelium develops immediately. Both freezing and heating apparently inhibits immediate development of such vegetative mycelium.

The first signs of the development of the sclerotia are small, white knots of mycelium formed by aggregation of hyphal cells. These knots take on a hemispherical or ellipsoid shape and swell by multiplication of the constituent cells forming a pseudo-parenchymatic tissue. Gradually the outer cells become pigmented but this is masked by the superficial hyphae growing over their surface. The outer surface of the sclerotial primordia becomes convoluted and gradually more strongly pigmented. The superficial hyphae become sloughed off exposing the now mature sclerotia which may be up to 5 mm broad. Where the sclerotium is raised from the agar-surface pigmentation takes place; the inner tissue remains compact, white and composed of small, hyaline, thin-walled cells. In large sclerotia the central area collapses and becomes hollow; the innermost layer of cells in these instances may also become thickened and pigmented (Plate 4 A-E).

STRUCTURE OF THE RHIZOMORPHS AND SCLEROTIAL PLATE.

Three distinct structures were found in Type II isolates : (1) hard, brown or black, cylindrical or flattened strands with pale tips formed in the agar or lifting the agar and growing between the lower surface of the agar and the Petri-dish surface, (2) softer white, flattened strands formed deep in the medium; and (3) red-brown thick, crust-like plates which radiate out from the original inoculum. The last structure also forms on the surface wherever the rhizoids reach the surface; they emerge and ultimately cover the entire agar surface (Plate 1 A & B).

The outer edge of the young rhizomorphs consists of narrow hyphae some of which project outwards to give an irregular fringe surrounding the developing rind (Plate 2 E; Plate 3 E & F) incl. microstructures. The individual members of the fringe may be septate or not, are encrusted by a layer of fine needle-like crystals often accompanied by irregular, granular crystalline material (Plate 2 D & Plate 4 F) and the base is usually swollen at the insertion of the hyphae into the rind (Plate 3 f). In older rhizomorphs this mantle is sparse or even absent and the outer layer is thin and composed of thick-walled hyphae 4-7 µm wide, more or less elongated in the direction of the axis of the rhizomorph (Plate 2 B & C). The medulla enclosed by the rind is composed of hyaline, thin-walled hyphae enlarging from the outer most part of the central area where they often break-down at maturity to give an irregular hole. Branching is accompanied by an abundant growth of the mantle marking the pushing out of the rind-cells. The rind at the apex of both branches and leader is pale in colour at first, ivory then cream, pale cinnamon and then red-brown as one progresses back from the tip or as one particular area matures.

The paler rhizomorphs are similar in structure to the apices of the branches and never seem to mature further. All the cells are hyaline and more regular and uniform in form than in the darker rhizomorph; only a small proportion of the cells darken.

The sclerotial crust (Plate 3 H) is apparently a modified rhizomorph in structure with only one pigmented, rind-like surface. The mantle is present although reduced; the rind consist of pseudoparenchymatous dark red-brown cells; the innermost zone, equivalent to the medulla in the rhizomorph, is composed of irregularly arranged hyaline cells many of which radiate downwards into the agar material.

The rhizomorph agrees in morphology with BREFELD'S description of *Rhizomorpha subterranea* and the paler 'rhizoids' with his *R. subcorticalis* both structures having been directly connected by him to *Armillaria* *mellea* fruit-bodies, on observation repeated on several occasions since by many authors.

DEVELOPMENT OF RHIZOMORPHS

The development of the rhizomorphs produced by the isolate Type II has been observed from mycelial aggregates, groups of hyphal tips and segments of rhizomorphs isolated from different parts of the system. From hyphal tips a small, entirely pale pinkish cinnamon-colour, or pale buff-colour colony is produced. It is only when the colony is above 5 mm in diameter and 7-days old that small dark areas and small, pale coloured compact areas are produced; often these are associated with microsclerotia with tufts or fans of pinkish buff or lilaceous buff hyphae heavily encrusted with crystalline material. The small areas of limited pigmentation produce rhizomorphs which spread out at the edge of the colony associated with the production of more hyphal tufts; in some cultures the rhizomorphs keep pace with the development of aerial and submerged mycelium or in others fail to develop further. No further rhizomorph formation usually takes place. However, the Michigan isolate showed rapid terminal extension of the rhizomorph with only occasional dichotomus or palmate branching and relatively little lateral rhizomorph development. Behind the growing point small, lateral individual hyphae grow out at right angles forming a hairy fringe and giving the agar a rather greasy appearance. Behind the growing tip the hyphae become multicellular, branched and encrusted with crystalline material. Under certain conditions which have not yet been determined a red-brown sheet forms over the lateral hyphae as an arched structure and gradually envelops most of the lateral hyphae. Such sheets also form where the rhizomorphs become erect and push out of the agar, and by futher growth the plates coalesce destroying the basic radiate pattern of the culture by joining the areas between the rhizomorphs. These plates, which are pseudosclerotial in structure are covered in small tufts of pinkish cinnamon hyphae (Plate 1 A & Plate 4 G). It was hoped that these were primordia and would ultimately produce some sort of fructification. This has not been so, indeed careful examination showed that all such structures have few similarities with primordia. The under surface of the pseudosclerotial plate is white. It is the aerial mycelium and the lateral hyphae which were clearly luminescent within a few minutes of the eyes becoming accustomed to the dark.

The terminal part of the rhizomorph is pale coloured and not just a simple aggregation of vegetative hyphae as is found in *Agrocybe* spp.

The actual tip contains a growing point of small isodiametric cells covered by an interwoven mass of hyphae. Larger cells are found in the middle of the outer zone and probably reflect the capacity of these rhizomorphs to transport food material which is recorded in the literature. In the pattern described above the Type II isolates agree in most respects with obeservations on *Armillaria mellea* described by SNIDER (1959) and GARRETT (1944 and 1953).

Discussion.

It is here proposed that the carpophoroid *Entoloma abortivum* is induced by an attack by the basidiomycete *Armillaria mellea.* They are therefore monstrosities even though some produce basidiospores, the viability of which have not been tested. The *A. mellea* apparently does not kill the fruit-body as actively growing mycelium of *E. abortivum* is always present and the carpophoroid does not putrefy any quicker than the agaricoid form. Therefore it would appear that there is some stimulant to growth either induced by *Armillaria mellea* or retained by the *Entoloma abortivum.* It is highly improbable that this is a widespread phenomenon amongst the agarics, even in the single family Rhodophyllaceae and it is hypothesised that the *Entoloma abortivum* provides some attractant to *A. mellea. Armillaria mellea* in its widest interpretation is such a common fungus that if it were possible to form such an association with other agaric-species one would have thought it would have been recorded on other occasions. *Entoloma abortivum* has not been fructified in culture and so infection has not been observed but by further experimentation and suitable manipulation it may be possible to induce *Armillaria mellea* to grow on other agarics which normally fruit easily in culture.

Armillaria mellea has been shown under certain circumstances to be a mycorrhizal associate although it is more commonly known as a parasite and probably in the field found most commonly as a saprophyte. It has been reported as the active endophyte in *Gastrodia elata* (Orchidaceae) by KUSANO (1911) in *G. cunninghamii* by CAMPBELL (1961) and in *Galeola septentrionalis* (Orchidaceae) by HAMADA (1939), and in *Monotropa* (Ericaceae) also by CAMPBELL (1971). In the first family it is apparently necessary for the stimulation of flowering; it would appear that the orchid is parasitic on the fungus.

When *Armillaria mellea* grows on woody debris it can spread out by the characteristic rhizomorphs to colonise other debris, and indeed from this source of food it can attack living plants producing wilt and subsequent death (THOMAS, 1934). A whole series of hosts have been recorded including Gymnosperms, Dicotyledons and Monocotyledons, trees, shrubs or even crop plants e.g. potato (RAABE, 1962; BAKER, 1972). Much work has been carried out on the development, of the rhizomorphs of *Armillaria mellea.* eg. GARRETT (1953), MOTTA (1967, 1969a, 1969b), REITSMA (1931) and SNIDER (1959), covering various aspects of cytology, anatomy, physiology etc. and whose biology assisted GARRETT in the formulation in the hypothesis of inoculation potential for plant infection. Our isolate from *Entoloma abortivum* agrees admirably with the many illustrations and descriptions which appear in their texts.

It has been known for some time that certain Ascomycetes will produce sexual stages only in the presence of other Ascomycetes or Hyphomycetes eg. *Melanospora pampeane* Speg. and *Fusarium moniliforme* Sheldon — for a review see L. HAWKER (1950). Frequently a pair of Ascomycetes in culture may grow together in such unison that it is difficult to detect the presence of one of the partners. This may also be exhibited with different species of Basidiomycete where from the growing margin of a culture one is able to isolate either one or other component eg. *Psathyrella coprophila* Watling and *Coprinus pellucidus* Karsten. The species do not appear to be competing against each other but rather act as a balanced association within a single ecosystem utilising nutrients etc., or perhaps even assisting one another. The pattern is further extended in observations by R.F.O. KEMP (see WATLING, 1971) where complex fruit-bodies have been found in *Coprinus* containing hyphae of two species; hyphae of the species for which the sexual stage is morphologically expressed and the hyphae of a similar autonomus species apparently unexpressed in the external morphology of the fruit-body. This is somewhat disturbing for those who require to recognise and classify species, but it must be emphasised that in the examples so far examined the fungi involved have very similar gross morphology; this has been found in nature and so is not a cultural phenonemon.

It has been recently shown that certain Basidiomycetes, particularly woodinhabiting species exist as partial parasites (GRIFFITH & BARNETT, 1967); thus *Pleurotus ostreatus* (Jacq ex Fr.) Kummer, the Oyster mushroom, which is frequently seen on old wood, utilises the hyphae of other fungi for growth. A vast array of behaviour-types is therefore exhibited in the higher fungi and within such a frame-work the activity of *Armillaria mellea* and *Entoloma abortivum* is no longer obscure.

It has now been shown by ROSINSKI & ROBINSON (1968), MACKNIGHT (1971) and WATLING (1971), in a resurgence of interest in the study of gastroid forms in culture that even simple changes in environment can upset the development of the agaricoid fruit-body. This present study offers an extension of our knowledge and is here presented as a further example of material which might be used in studying secotiaceous/agaric relationships but whose formation can be monitored and considered from a rather different approach to the vast amount of purely morphological work in the literature. Only one other agaric has been observed in the field to produce almost identical carpophoroids *i. e., Inocybe geophylla* Watling 6582 & 6658 ; on leafy debris in mixed woodland in deep shade Boyne Highland, Emmet Co. Michigan U.S.A. This is probably a unique collection and was apparently not associated with *A. mellea*[1].

It has not been possible so far to fruit *Entoloma abortivum* in culture either on the various media available, or with the various treatments suggested in the literature ; it has also been impossible so far to fruit *Armillaria mellea* under artificial conditions[2]. Even if *E. abortivum* were successfully fructified in pure culture it would be very doubtful if the carpophoroid could be obtained except after very extensive trials, as the pattern of development and progress of the mycelium must be delicately balanced and at the moment we know so little about fruit-body initiation in the agarics under normal conditions. Thus KOCH'S law has not been fulfilled but I believe the above observations indicate the mechanism to be found in nature.

It is proposed that the hyphae of *Armillaria mellea* upset the developmental pattern of the fruit-body and from fresh and herbarium material it can be shown that this can be interfered with at various stages in the growth of a primordium and young fruit-body. The development of *Entoloma abortivum* is gymnocarpic and apparently the pileus does not expand whilst the gills try to develop over the entire or part of the pileus-surface. A similar phenonemon is found in the morchelloid forms of *Psilocybe merdaria* where the sterile pileus-surface is considerably reduced. The gills are replaced in *E. abortivum* carpophoroids by a friable tissue and it was this hyphal aggregate which in the introduction was termed « veil-like tissue ». This structure resembles the « veil » found stretching across the « gills » in *Lentodium squamulosum* Morgan giving the under surface of this fungus a fenestrate appearance. In *E. abortivum* this tissue apparently originates from growth of the tomentum at the stipe-base. The tomentum, the « veil-like tissue » and mycelial cultures from the agaricoid fruit-body are similar in all morphological ways.

---

[1] It is interesting to note that SINGER (1970) has recently described carpophoroids in *A. mellea* from Illinois, U.S.A.

[2] During the preparation of this manuscript RAABE (1972) fructified one strain of *Armillaria mellea* on *Ficus* wood.

The stipe in the carpophoroid does not develop much more than simply to become a small dome of tissue which may or may not swell; the lower area of the ovoid column becomes densely coated with white mycelium which often envelopes some of the areas which would have been spore-bearing.

In other instances the pileus is formed with the gills beneath but both are hypertrophied and the latter wrinkled and fleshy. The pileus-margin in this case is often incurved by the swelling.

TAXONOMIC IMPLICATIONS

FRIES in 1821 erected the groupings of *Leptonia, Eccilia* and *Nolanea,* and subsequently (1838) propose *Entoloma.* He finally proposed the genus *Acurtis* eleven years later in Summa Vegetabilium, establishing as its type, *A. giganteus* based on *Clavaria gigantea* Schweinitz 1822, assumed by some mycologists to be the carpophoroid state of *Entoloma abortivum.* Subsequently in addition to FRIES groupings W.G. SMITH described *Agaricus* subgenus *Claudopus* (1870) a name which GILLET (1876) later used for a genus of laterally stipitate members of the group. KUMMER in 1871 raised all FRIES' *Leptonia, Eccilia, Nolanea* and *Entoloma* to generic rank. All these groupings, excepting *Acurtis,* have long been adopted in Europe as being natural genera based on pileus texture, attachment of the gills etc — and later on basidiospore morphology and structure of both the hymenophoral trama and pileipellis. They were later grouped in the family Rhodophyllaceae; some authors, following QUÉLET, prefer to recognise only a single genus and utilise the name *Rhodophyllus,* 1886, for the whole group. The name *Rhodophyllus* is untenable on nomenclatural grounds, see DONK (1949 and 1962), and to others on taxonomic grounds, see ORTON (1960). LARGENT & BENEDICT (1970) have recently published as an addition to the group the genus *Alboleptonia; Leptoniella* was also introduced by another North American author, EARLE (1909) but it has never been taken-up in Europe.

The history of the genus *Acurtis* is complex and has created much heated discussion. Based on *Clavaria gigantea,* it was included in the Elenchus by FRIES (1828) under this original name; it was not until twenty years later did he establish the genus *Acurtis* for this fungus but continued to assign it to the « Clavariaceae » (in Summa Veg. Scand.) as the link between *Sparassis* and *Clavaria.*

BURTT (1922) examined the type of *Clavaria gigantea* in the Curtis herbarium (FH) but he was neither able to find basidia nor any basidiospores which would have indicated or confirmed affinities, nor did he find any fruiting tissue which would allow the fungus to be classified. It was at the same time that BURTT pointed out that the fungus *Entoloma abortivum,* then classified in the genus *Clitopilus,* frequently could be found occurring dimorphically in Eastern United States and offered the opinion that *Acurtis gigantea* was in fact the carpophoroid state of this fungus.

SINGER (1962) has also examined the type material and he too was unable to find basidia or basidiospores; HESLER whilst preparing his monograph of S. Eastern American species of *Entoloma* sectioned the type-material also with similar results. Thus the type is apparently sterile but SINGER (1962) has found basidiospores in other specimens of the carpophoroid and concludes *Acurtis* and the carpophoroid stage of *Entoloma abortivum* are one and the same fungus. Whilst basidiospores have been found on both dimorphs during the present study it is suggested here in contradiction to SINGER (1962) that *Acurtis* is the valid generic name for neither *Rhodophyllus* (1886) nor *Entoloma* emend Donk (1949).

HESLER (1967) introduces two arguments (i) the type of *Acurtis* is composed of carpophoroids and are not of the usual agaricoid form, and (ii) type studies indicate that these same fruit-bodies are sterile. Thus if *Acurtis* is indeed the same as *Entoloma abortivum* it cannot be used as it is based on a monstrosity (International Code of Bot. Nomenclature Article 67) and the type is sterile (Int. Code Bot. Nomen. Article 5 a). It is, however, doubtful whether *Acurtis* in fact does belong to *Entoloma. Clavaria gigantea* was originally described as a large receptacle, as large as a man's head and this is several fold greater than the largest dimensions of the carpophoroids of *Clitopilus abortivus.*

Parasitised fruit-bodies of the bolete *Tylopilus rubrobrunneus* Mazzer & Smith however, which have also been described from Eastern North America do resemble a man's head; from my own collections of this same species of bolete the dimensions are in keeping with those of *Acurtis gigantea* (see Mazzer & Smith, 1967). Moreover the experimental work described above indicates that *Armillaria mellea* plays a key-part in the development of the carpophoroid state in *Entoloma abortivum* and therefore the carpophoroid fruit-body must be considered an abberant structure.

The following synonymy is proposed :

Entoloma abortivum (Berkeley & Curtis) Donk in Bull. Bot. Gdn. Buitenzorg IIV 18: 157, 1949.

Basionym: *Agaricus abortivus* Berkeley & Curtis in Ann. Mag. Nat. Hist. III, 4: 289, 1859.

Clitopilus abortivus (Berkeley & Curtis) Saccardo in Sylloge Fungorum 5: 701, 1887.

Pleuropus abortivus (Berkeley & Curtis) Murrill in Mycologia 2: 280, 1911.

Rhodophyllus abortivus (Berkeley & Curtis) Singer in Revue Mycologie, 5: 9, 1940.

Synonym: *Acurtis gigantea* (Schweinitz) Fries,
sensu Burtt in Ann. Miss. Bot. Gdn., 1922.
sensu Singer, Agaricales in Modern Taxonomy, Edition 2, 1962.
sensu Hesler, Entoloma in South eastern North America in Beih. Nova Herwigia, Heft 23, 92, 1967.

ACKNOWLEDGEMENTS

My thanks are here expressed to Miss J. EVITT for her patient assistance in the laboratory, to Profs. L. HESLER and O. K. MILLER for supplying herbarium material and to Profs O. K. MILLER & H. BIGELOW for supporting some this material with cultures. I also wish to thank Prof. A. H. SMITH for his stimulating discussions on this subject, and encouragement for the completion of the work.

REFERENCES

BAKER J. J., 1972. — *Report* on *diseases of cultivated plants in England and Wales for the years* 1957-68. Technical Bulletin 25, Min. of Agric. - Fisheries & Food, London.

BREFELD O., 1877. — *Bot. Untersuchungen uber Schimmelpilze*, Heft 3, Leipzig.

BURTT E. A., 1922. — North American species of *Clavaria, Ann. Miss. Bot. Gdn.*, 9. 1-78.

CAMPBELL E. O., 1961. — Mycorrhiza of *Gastrodia cunninghamii, Trans. Roy. Soc. New Zealand* N.S.I. 289-296.

CAMPBELL E. O., 1971. — Notes on the fungal association of two *Monotropa* Species in Michigan. *Mich. Bot. 10.*, 63-66.

DONK M. A., 1949. — Nomenclatural notes on generic names of agarics, *Bull. Bot. Gdns. Buitenzorg*, Series III, 18, 83-168.

DONK M. A., 1962. — The generic names proposed for Agaricaceae, *Beih. Nova Hedwigia*, Heft 5, Weinheim.

EARLE S., 1909. — The genera of the North American Gill fungi, *Bull. New Work Bot. Gdn.* 5: 424, 373.

FRIES E. M., 1821. — *Systema mycologicum*, Lund.

FRIES E. M., 1828. — *Elenchus fungorum*, Uppsala.

FRIES E. M., 1838. — *Epicrisis systematis Mycologici*, Uppsala.

FRIES E. M., 1849. — *Summa Vegetabilium Scandinaviae*, Holmiae & Lipsiae.

GARRET S. D., 1944. — *Root disease fungi*, Chronica Botanica, Waltham.

Garret S. D., 1953. — Rhizomorph behaviour in *Armillaria mellea* (Vahl) Quél. i. Factors controlling the rhizomorphs initiation by *A. mellea* in pure culture, *Ann. Bot.*, NS. 17, 63-79.

Gillet C. C., 1876. — *Champignons de France, Hymenomycetes*, Paris.

Griffith N. T. & Barnett H. L., 1967. — Mycoparasitism of Basidiomycetes in culture, *Mycologia* 59, 141-154.

Hamada M., 1939. — Studien über die mycorrhiza von *Galeola septentrionalis* Reichb. f. Ein neuer fall der Mykorrizabildung durch intraradicale Rhizomorpha, *Jap. Journ. Botany* 10, 151-211.

Hamada M., 1939. — Physiologisch morphologische studien über *Armillaria mellea* (Vahl) Quélet nit besonderer Rucksicht auf die Oxalsäurebildung : Ein Nachtrag zur mykorriza von *Galeola septentrionalis* Reichb. f., *Jap. Journ. Botany* 10, 387-463.

Hawker L. E., 1950. — *Physiology of Fungi*, London.

Hesler L. R., 1967. — *Entoloma* in south eastern North America, *Beih. Nova Hedwigia*, Heft 23., Lehre.

Kummer P., 1871. — *Führer in die Pilzkunde*, Zerbst.

Kusano S., 1911. — *Gastrodia elata* and its symbiotic association with *Armillaria mellea*, *Journ. College Agric. Tokyo* 4, 1-66.

Largent D. L. & Benedict R. G., 1970. — Studies in the Rhodophylloid fungi II, *Alboleptonia*, a new genus. *Mycologia* 62, 437-452.

McKnight K. 1971. — Cultural studies of *Psilocybe* I., Variation in a new species of the *P. coprophila* group. *Bull. Torrey. Bot. Club*, 98 (1), 4-34.

Mazzer S. J. & Smith A. H., 1967. — New and interesting boletes from Michigan. *Mich. Bot.* 6, 57-67.

Motta J., 1969 a. — Somatic nuclear division in *Armillaria mellea*, *Mycologia* 61, 873-886.

Motta J., 1969 b. — Cytology and Morphogenesis in *Armillaria mellea*, *Amer J. Bot.* 56, 610-619.

Orton P. D., 1960. — New Check List of British Agarics and Boleti Part III ; Notes on genera and species in list, *Trans. Brit. Mycol. Soc.* 43, 137-439.

Petersen R., 1971. — Editor - *Evolution in the Higher Basidiomycetes*, Knoxville.

Quélet L., 1886. — *Enchiridion fungorum in Europa media et praesertim in Gallia vigenium*, Lutetia.

Raabe R. D., 1962. — Host List of the root rot fungus *Armillaria mellea*, *Hilgardia* 33 (2), 25-88.

Raabe R. D., 1972. — Variation in pathogenicity and virulence in single-spore isolates of *Armillaria mellea*, *Mycologia* 64, 1154-1159.

Reitsma, von J., 1931. — Studien über *Armillaria mellea* (Vahl) Quél. Mitteilung aus dem Phytopathologischen Laboratorium Willie Commelin Scholten Baarn, *Phytopath. zeitsch.* 4, 461-522.

Ridgway R., 1912. — *Color standards and nomenclature*, Baltimore.

Rosinski M. A. & Robinson A. D. — 1968. — Hybridization of *Panus tigrinus* & *Lentodium squamulosum*, *Amer. J. Bot.* 55, 242-246.

Schweinitz L. D. v., 1822. — Synopsis Fungorum carolinae superioris, *Schrift. d. Naturforsch. Ges. Leipzig.* Schrift 1 : 113.

Singer R., 1962. — *The Agaricales in modern Taxonomy*, Weinheim.

Singer R., 1970. — *Armillariella mellea*, *Schw. Zeits Pilzk.*, 48, 25-24, 65-69.

Singer R., 1971. — in Petersen R. see above.

Smith, Worthington G., 1870. — Clavis Agaricinorum, Series II - V. *J. Bot. Lond.* 8, 213-223.

Snider P. J., 1959. — Stages of development in rhizomorph thalli of *Armillaria mellea*, *Mycologia* 51, 693-707.

Thomas H. H., 1934. — Studies on *Armillaria mellea* (Vahl) Quél. Infection, parasitism and host persistance. *Journ. Agric. Res.* 48, 187-218.

TOWNSEND B. B., 1954. — Morphology and development of fungal rhizomorphs, *Trans. Brit. Mycol. Soc.* 37, 222-233.

WATLING R., 1971. — Polymorphism in *Psilocybe merdaria*, *New Phytol.* NS 70, 307-326.

WATLING R., 1971. — Methods in Microbiology Vol. 4 editor C. Booth. Chapter 8, Basidiomycetes : Homobasidiomycetidae, 219-236, London.

Royal Botanic Garden,
Edinburg EH 3 5 *LR*
(Grande-Bretagne).

SOCIETE LINNEENNE DE LYON

33, RUE BOSSUET — 69006 LYON

Commission paritaire n° 52 199
Le gérant : Marc Terreaux