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TAXONOMIC AND BIOLOGICAL OBSERVATIONS ON THE GENUS LICHENOCONIUM (SPHAEROPSIDALES)

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(With 2 Text-figures, 5 Tables and Plates 21–29)

A revision of the genus *Lichenoconium* Petr. & Syd. (Sphaeropsidales) is presented. Ten species are accepted including *L. echinosporum* D. Hawksw., *L. erodens* M.S. Christ. & D. Hawksw. and *L. parasiticum* D. Hawksw. *sp. nov.* and *L. cargillianum* (Linds.) D. Hawksw. and *L. usneae* (Anzi) D. Hawksw. *combs. nov.* All species apart from *L. boreale* (Karst.) Petr. & Syd. are exclusively lichenicolous and species of the genus certainly occur on 58 host lichens (with unconfirmed reports for a further 11). Up to three *Lichenoconium* species can occur on a single host but when this arises different symptoms often result. Descriptions of the accepted species and details of the reactions of various hosts to them are presented; a key and table summarising their differences is included. The species are delimited on the basis of their anatomy and morphology without regard for the host genera infected; some then prove to be restricted to particular host genera whilst others occur on several. The identities of five excluded taxa are discussed, and it is emphasized that as currently conceived the genus is not natural and that both *L. boreale* and *L. pertusariicola* (Nyl.) D. Hawksw. will eventually require transference to other genera when generic concepts in allied non-lichenicolous fungi have been clarified. Scanning electron micrographs of conidia of most species treated are included.

The systematics of lichenicolous Deuteromycotina (Fungi Imperfecti) has received scant attention in recent decades and the taxonomy of most imperfect fungi growing on lichenized fungi is consequently in an unsatisfactory state. Those lichenicolous fungi forming single-celled dark brown conidia in irregularly opening pycnidia were referred to *Coniothyrium* Corda by most earlier workers and Keissler (1910) accepted four lichenicolous species and one variety in that genus based on differences in spore shape, colour and the reaction of the host to the invading fungus. Vouaux (1914), in his conspectus of lichenicolous fungi then recorded throughout the world, accepted nine species and one variety within *Coniothyrium* of which four were newly described. The non-lichenicolous *Coniothyrium* species were not considered to be congeneric with the lichenicolous ones by Petrak & Sydow (1927) primarily because of the absence of a

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clearly differentiated ostiole in the latter which tend to discharge their conidia through an irregularly formed apical opening. These authors introduced the new generic name *Lichenoconium* to accommodate these fungi and included five lichenicolous and two non-lichenicolous species within it. *Lichenoconium* was taken up by Keissler (1930) in his monograph of the central European lichenicolous fungi (although he retained one species in *Coniothyrium*) where he recognised five species and one variety. In contrast to Vouaux (1914) and Petrak & Sydow (1927), Keissler appears to have separated his species primarily on the basis of the different host species involved rather than on the characters of the fungi themselves.

In more recent years, apart from papers discussing particular species or reporting new localities and hosts (e.g. Christiansen, 1956; Galløe, 1954; Hawksworth, 1975, 1976; Santesson, 1960), no re-appraisal of this group of fungi has been made. Clauzade & Roux (1976) include keys to eight species based largely on the concepts of Keissler and Vouaux but theirs was an uncritical compilation.

During my own studies of lichenicolous fungi both in the field and the herbarium numerous collections came to light from hosts from which no *Lichenoconium*-like fungi had previously been reported or which differed in some details from the published descriptions; furthermore, some morphologically and anatomically separable fungi of this genus were found to occur on the same host species. The present contribution represents an attempt to produce a morphologically and anatomically based, as opposed to a host-based, taxonomy for the lichenicolous fungi referred to *Coniothyrium* and *Lichenoconium*. In addition to material present in British herbaria and type and authentic material received on loan from various institutions, I have been fortunate in being able to examine the important collections of fungi of this group made by Dr. M. Skytte Christiansen, Prof. Dr. J. Poelt, Prof. Dr. R. Santesson (those in UPS), and Dr. A. Vězda; some 190 collections of *Lichenoconium*-like fungi were studied microscopically in the course of this investigation.

ANATOMICAL AND MORPHOLOGICAL CHARACTERS

In order to determine the characters likely to be most valuable for species delimitation in the group it was first necessary to examine those that are available and assess their potential value. At an early stage in these investigations it soon became evident that, in addition to the species requiring exclusion for a variety of reasons (see pp. 192–194), *Lichenoconium boreale* and *L. pertusariicola* were not congeneric with the bulk of the taxa requiring consideration. These two species differ in a large number of characters both from each other and from the other species treated here and have been retained in *Lichenoconium* only as an interim measure in view of the large number of names in generic rank already published for non-lichenicolous members of the Sphaeropsidales with brown and simple conidia whose application is uncertain at the present time; the differences are summarised under the discussions of them and they will consequently not be considered further in this section.

Pycnidia.

The pycnidia of *Lichenoconium* were distinguished from those of *Coniothyrium* by having an irregular opening and not a well-defined ostiole by Petrak & Sydow (1927) and this appears to have been their main reason for recognising *Lichenoconium* as a separate genus. This character is well seen in the older pycnidia of those species with large pycnidia (e.g. *L. lichenicola*, *L. cargillianum*, *L. xanthoriae*) but less marked in those with smaller fruits (e.g. *L. erodens*) and is a good field-character for the recognition of the group as the openings are generally visible with a ×20 lens. Within a single species, and within different pycnidia in the same collection, there is a considerable variation in the size of the opening, its regularity, and even its presence in young pycnidia. The opening appears to develop by a breakdown of the tissues in the upper part of the pycnidial wall; this is often irregular and so gives the opening uneven edges. As the pycnidia age they tend to become increasingly open and in most species can eventually assume a cupulate or disc-like form which in section can lead them to having an almost Melanconiaceous appearance in which the conidiogenous cell layer is exposed rather than enclosed.

The degree of opening seems to be of little taxonomic value in the group in view of the variability even within single collections but the maximum size which the pycnidia attain does appear to be important. Pycnidial size is a character which might be expected to be host-influenced but in *Lichenoconium* this does not seem to be the case as there are instances of different species with differently sized pycnidia (differing also in other characters) occurring on the same host species and together on the same specimen but remaining quite distinct.

The pycnidial wall appears to be more variable with respect to the numbers of layers of cells comprising it and the extent to which their walls become thickened but in all instances is pseudoparenchymatous (paraplectenchymatous) rather than prosenchymatous (apart from *L. boreale*) in structure. Considerable variation in the extent to which the pycnidial wall cells become thickened is seen in different vertical sections of the same species within a single apothecium or thallus lobe and appears to be strongly related to the age of the pycnidium itself, younger pycnidia tending to have walls of less strongly thickened cells. The outer layers of the wall are consistantly darkly pigmented (apart from *L. pertusariicola*) and while an inner layer(s) of hyaline cells is usually present, in some cases the conidiogenous cells may arise directly on darkly pigmented cells so that a separate hyaline inner layer cannot be distinguished.

Conidiogenous cells.

The conidiogenous cells in all species (Figs. 1, 2) are essentially phialidic but in almost all of them these may percurrently proliferate and so produce annellide-like conidiogenous cells. The distinction between annellidic and phialidic conidiogenous cells has already been the cause of considerable debate (see Morgan-Jones *&* *al.*, 1972; Kendrick, 1971) and it seems unlikely that an entirely satisfactory definition will be derived in the near future. Within individual collections of *Lichenoconium* both non-proliferating and proliferating phialides often occur within the same pycnidium while in some specimens no proliferation may be evident at all. In general it is the youngest

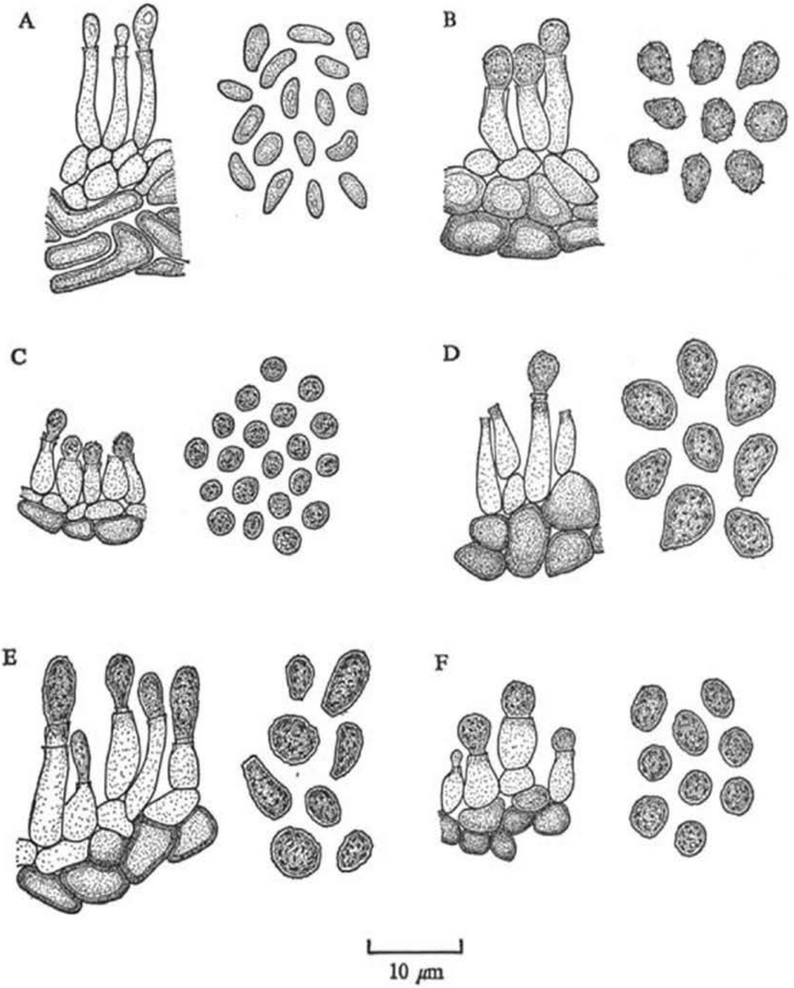

Fig. 1. Conidiogenous cells and conidia of *Lichenoconium* species. — A. *L. boreale* (holotype). — B. *L. echinosporum* (holotype). — C. *L. erodens* (holotype). — D. *L. cargillianum* (holotype). — E. *L. lichenicola* (holotype). — F. *L. parasiticum* (*IMI 192264*).

pycnidia in which no proliferation can be detected and any attempt to split specimens of this group on the basis of the presence or absence of annellations would be unsatisfactory as it would lead to the separation of taxa otherwise identical and able to cause identical symptoms on particular hosts.

Most previous workers on *Lichenoconium* have had difficulty in seeing the conidiogenous cells and so they have often been poorly described and measured. In the present studies squashing a single moistened pycnidium (removed under a dissecting microscope) in a solution of 0.5 g erythrosin in 100 ml of 10% ammonia proved a most satisfactory technique for their examination and showed details of the hyaline apical structures of the conidiogenous cells more clearly than a range of other mounting media tested. The conidiogenous cells (other than in *L. boreale* and *L. pertusariicola*) are short-cylindrical but become somewhat swollen below to give a rather ampulliform appearance. The cells are mainly hyaline but at the apex can become pigmented to varying extents and also assume a somewhat verruculose ornamentation apparently identical to that developing on the conidia themselves. This pigmentation varies considerably even within a single pycnidium and seems to be of little taxonomic importance although it is much more frequently developed in some species (e.g. *L. lichenicola*, *L. cargillianum*, *L. usneae*) than in others (e.g. *L. erodens*, *L. parasiticum*).

The lengths of the conidiogenous cells proved to be of some taxonomic value in the group and, to judge from occurrences on the same host, not host determined. They are shortest in *L. erodens* and *L. parasiticum*, where they may be only of about the same height as the diameter of the conidia, but in most species are 1½—2 times the size of the conidia.

Conidia.

The conidia in all cases arise singly from the apices of the conidiogenous cells and become pigmented prior to their separation (except in *L. boreale*). They are non-septate, brown, and generally not evidently guttulate. While in most species the conidia are globose or subglobose they are not invariably so and in *L. lichenicola* in particular tend to be elongate-clavate and in *L. pyxidatae* tend to be broadly truncated. Even in species normally with almost globose conidia, occasional elongate-clavate conidia are sometimes to be found (e.g. in *L. usneae*); such conidia tend to be larger than usual for the species as well as of a somewhat unusual shape but occur at low frequencies and seem to be abnormally developed by the conidia failing to secede normally and remaining attached to the conidiogenous cells longer than is usual. These abnormal conidia do not appear to be taxonomically important.

Conidial size, excluding the size of abnormal conidia, proved to be of major taxonomic value in *Lichenoconium*, even though there is some degree of overlap in the size ranges of different species and minor variations on different hosts (see Tables IV and V). Differences in this feature proved to be correlated with other characters, such as conidiogenous cell size, pycnidial size, and symptoms on the host.

The conidia in all species (except *L. pertusariicola*) can be seen to have some type of ornamentation by light microscopy at high magnifications but the coarseness of this varies considerably; those of *L. lichenicola* and *L. cargillianum* being particularly coarse

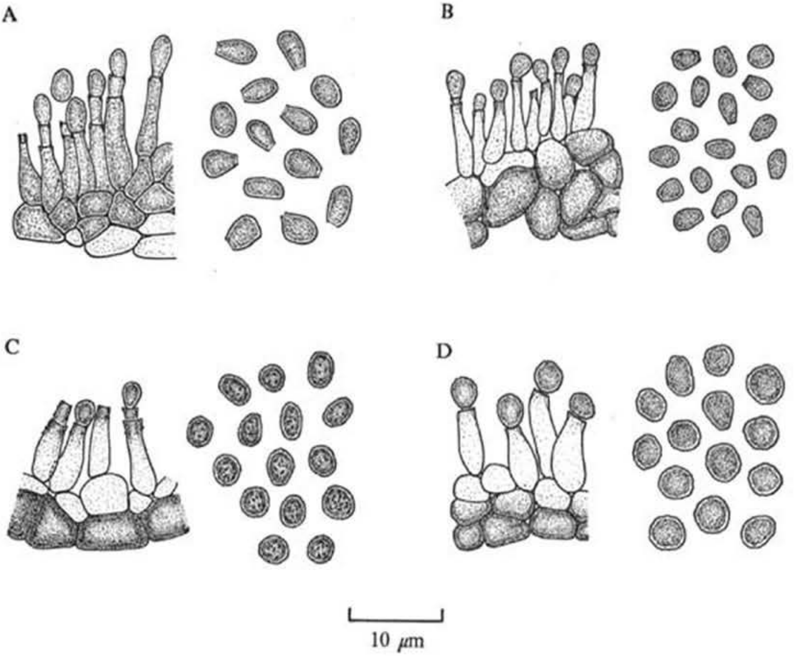

Fig. 2. Conidiogenous cells and conidia of *Lichenoconium* species. — A. *L. pertusariicola* (*IMI 186240*). — B. *L. pyxidatae* (holotype). — C. *L. usneae* (isotype). — D. *L. xanthoriae* (holotype).

and those of *L. pyxidatae* (and *L. boreale*) relatively smooth. In order to determine the nature and extent of conidial ornamentation selected specimens were examined in a scanning electron microscope. Most species were found to have a distinctly verruculose ornamentation varying in degree rather than type (Pls. 24A, 25B, 27C—D, 28H—I) but in *L. echninosporum* the ornamentation was more widely spaced and delicate giving its conidia a more echinulate appearance. (In *L. pertusariicola* the conidia proved to be entirely smooth-walled, Pl. 29E, while in *L. boreale* they were densely verruculose but more delicately so, P. 21E.) In view of the small number of specimens it was possible to examine by scanning electron microscopy it would be premature to place much emphasis on some other variations in the conidia which became apparent, viz. the appearance of the scar formed when they became separated from the conidiogenous cells which is broadly truncate in *L. lichenicola*, for example, but appears as a small circular depression in the globose-spored species (e.g. *L. parasiticum*, Pl. 27D); the latter may perhaps arise from a rounding-off of the conidium following seccessation, but detailed ultrastructural studies will be necessary to verify if this is the case.

HOST RANGE AND PATHOGENICITY

From Table I it can be seen that *Lichenoconium* species are reliably recorded from some 58 lichenized species here and that there are unconfirmed reports for a further eleven hosts of which at least two are certainly erroneous. When the fungi are delimited on the basis of their anatomy and morphology without regard to the host (Table III and Key to the Species), it is necessary to accept that in some instances more than a single *Lichenoconium* can be associated with a particular host species and

TABLE I

SYNOPSIS OF THE KNOWN AND REPORTED LICHENS SUPPORTING LICHENOCONIUM SPECIES

* *Alectoria fuscescens* H
Anaptychia ciliaris H
(*Bacidia rubella*[1])
(*Buellia disciformis*[2])
* *Cetraria sepincola* I
* *Cladonia arbuscula* G, H
C. cariosa[3] H
C. cenotea G
C. chlorophaea G
C. fimbriata G
C. furcata G
  ssp. *subrangiformis* G
* *C. incrassata* G
* *C. pocillum* G
C. pyxidata G
(*Cornicularia aculeata*[4])
Evernia prunastri C, E
* *Heterodea muelleri* B
* *Hypogymnia bitteriana* C
* *H. physodes* C, H
* *Lecanora admontensis* E
* *L. chlarona* C
L. chlarotera E
(*L. concolor*[5])
L. conizaeoides E
(*L. intumescens*[5])
(*L. nitens*[5])
L. pacifica H
L. pallida E
* *L. polytropa* E
* *L. rubina* E
* *L. subcarnea* E
L. subfusca aggr. E
L. subfuscata E
L. superfluens E
(*L. symmictera*[5])
* *Parmelia borreri* E
P. conspersa H
P. exasperata H
P. galbina C, E
P. glabratula H
  ssp. *fuliginosa* H
P. olivacea H, I
* *P. pastillifera* E
P. perforata A
* *P. perlata* C
P. pulla H
* *P. rudecta* H
* *P. saxatilis* C, E, H
P. sulcata C, E
* *P. verruculifera* H
* *Parmeliopsis ambigua* C
Pertusaria hymenea C, F
P. leioplaca F
P. pertusa C, F
(*P. pustulata*[6])
(*P. texana*[7])
(*Physcia adscendens*[8])
P. aipolia D, H
* *P. stellaris* H
* *Physconia pulverulenta* H
(*P.* aff. *venusta*[9])
* *Ramalina* aff. *baltica* H
R. calicaris H
R. siliquosa H
* *R. subgeniculata* H
R. yemensis A
* *Squamarina lentigera* E
Usnea filipendula aggr. H
Xanthoria parietina I
X. polycarpa I

A = *L. cargillianum*; B = *L. echinosporum*; C = *L. erodens*; D = *L. lichenicola*; E = *L. parasiticum*; F = *L. pertusariicola*; G = *L. pyxidatae*; H = *L. usneae*; I = *L. xanthoriae*.

DOUBTFUL AND ERRONEOUS RECORDS (placed in parentheses): [1]*L. lecanoracearum* (Vouaux, 1914) probably an error for *Muellerella hospitans* Stiz.; [2]*L. lichenicola* var. *buelliae* (Keissler, 1910, 1930, etc.) host identity in need of confirmation (see p. 183); [3] also *L. cladoniae*, see p. 192; [4]*L. imbricariae* (Bachmann, 1926), see p. 186; [5]*L. lecanoracearum* (Vouaux, 1914), most probably refer to *L. parasiticum* but require confirmation; [6]*Coniothyrium harmandii* (Vouaux, 1914), see p. 194; [7]'*Coniothecium* sp.' (Dibben, 1974), see p. 183; [8]*L. lichenicola* (Vouaux, 1914), see p. 177; [9]*L. imbricariae* and *L. pyxidatae* (Vouaux, 1914), host and fungi require confirmation.

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* Host species reported for the first time here.

TABLE II

SYMPTOMS PRODUCED ON THE SAME HOST SPECIES BY DIFFERENT LICHENOCONIUM SPECIES

Host *Lichenoconium*	Symptoms
Cladonia arbuscula	
L. pyxidatae	podetia becoming discoloured
L. usneae	podetia becoming decolourised
Evernia prunastri	
L. erodens	thallus discoloured, no dark margin produced
L. parasiticum	thalli already in poor condition attacked, no special symptoms
Hypogymnia physodes	
L. erodens	black-margined necrotic spots formed on thalli, several pycnidia per spot, the centre of the spot eroding to leave a hole
L. usneae	infection not limited to spots, margin of infected area not blackened, pycnidia scattered, thallus not eroded
Parmelia galbina	
L. erodens	pycnidia in apothecia which are somewhat discoloured
L. parasiticum	pycnidia in apothecia which are somewhat discoloured
P. olivacea	
L. usneae	pycnidia in apothecia which become discoloured
L. xanthoriae	pycnidia in apothecia which become discoloured
P. saxatilis	
L. erodens	black-margined necrotic spots formed on thalli, several pycnidia per spot, the centre of the spot eroding to leave a hole
L. parasiticum	black-margined necrotic spots formed on thalli, one pycnidium per spot, the centre of the spot not eroding
L. usneae	pycnidia in apothecia which become somewhat discoloured (most often blackened)
Pertusaria pertusa	
L. erodens	infected parts of the thallus discoloured and killed
L. pertusariicola	infected parts not or only slightly affected

in Table II these instances are summarised. It is of interest to note that in many cases where different *Lichenoconium* species attack a particular host species either different symptoms are produced or different parts of the host colonized; such differences in host reactions lend support to a taxonomy based on the characters of the fungi themselves as it may be inferred from such observations that physiologic differences are correlated with the anatomical ones.

The extent to which particular *Lichenoconium* species are pathogenic to their hosts varies considerably between the species. In general *L. echinosporum* and *L. erodens* appear to be the most harmful and are clearly parasitic able to colonise young and healthily growing tissues which they often kill reducing the normal colour of the thallus to shades of brown or whitish-brown and forming extensive lesions in colonies. *L. parasiticum*, *L. pyxidatae* and *L. usneae* are apparently less strongly pathogenic and more regularly occur on tissues which are already unhealthy either through age, snail grazing, or attacks by other lichenicolous fungi: infected tissues are often localised and, while discolourisations of apothecia and the production of small necrotic patches on thalli are frequent symptoms, they are seldom associated with very extensive damage, although with heavy infections ascospore production may be reduced due to disruption of the thecial tissues. *L. xanthoriae* appears to cause very limited damage also unless the thallus is already unhealthy. But *L. pertusariicola* is perhaps best considered as a parasymbiont (i.e. symbiotic with a pre-existing symbiosis) as its hosts seem to be largely unaffected by its presence.

In considering the symptoms produced by a particular *Lichenoconium* on different hosts it is necessary to try to distinguish between those which are due to the fungi themselves and those which are reactions of the host to infections. The most common reaction to infection by the more pathogenic species in foliose lichens is the production of an area of dead tissue limited by a black band of varying thickness within which the infection is confined. The dark band in such cases appears to comprise hyphae of the host which become rather thicker walled and pigmented brown and is thus a host reaction. Similar spots can be formed by some of the hosts for *Lichenoconium* species in response to infections by quite different lichenicolous fungi (e.g. *Cornutispora lichenicola* D. Hawksw. & Sutton and *Phoma cytospora* (Vouaux) D. Hawksw. on *Parmelia sulcata*) and so the use of such characters in the formulation of the taxonomy for a particular group of lichenicolous fungi has to be cautious. In this respect it is, however, of interest to note that when *L. parasiticum* colonises *Parmelia saxatilis*, for example, single pycnidia become confined in strictly circumscribed black-bordered spots (Pl. 26E—F) similar to those formed by the same fungus on *P. sulcata* (Pl. 26G), but that *L. erodens* on *P. saxatilis* forms larger spots including several pycnidia similar to those it develops on *Hypogymnia* species (e.g. Pl 23A—C).

The extent to which the hyphae of the colonising fungi ramify amongst the host tissues is difficult to determine except for dark hyphae arising from the pycnidial wall which can be seen in sections in the immediate vicinity of the pycnidia. Hyphae belonging to the fungi may be encountered also on the surface of infected tissues, including thallus lobules (Pl. 26D) and apothecia; in the latter case these may partly

TABLE III

SYNOPSIS OF THE CHARACTERS SEPARATING THE SPECIES OF LICHENOCONIUM

Species	Pycnidia	Conidiog. cells (μm)	Conidia (μm)	Other diagnostic features
L. boreale	(100—)150—250	(8—)10—12 × 1—2(—2.5)	(2.5—)3—3.5(—4) × 1.5—2.5	Wall prosenplectenchymatous; conidia pale and rather smooth-walled, often reniform.
L. cargillianum	100—175(—200)	(7—)8—10(—12) × (2.5—)3—3.5	5—7(—7.5) × 3.5—5(—6)	Conidia particularly verruculose.
L. echinosporum	65—125	(7—)8—10(—11) × 2—3	4.5—5 × 3—4	Conidia with a characteristic sparsely echinulate ornamentation.
L. erodens	(20—)30—50(—60)	(3.5—)4—5(—6) × (2—)3—3.5(—4)	2—3.5(—4)	—
L. lichenicola	100—200	(6—)8—13(—14) × 2—3.5	(4—)6—8(—9) × 3—4(—6)	Conidia distinctly tapered at base.
L. parasiticum	(30—)40—80(—100)	(4—)5—7(—8) × (2—)3—3.5(—4)	(2.5—)3—4.5(—5.5)	—
L. pertusariicola	100—250(—325)	3.5—10 × 2—3	3.5—6 × 2.5—3.5	Wall cells hyaline; con. completely smooth
L. pyxidatae	(60—)80—120(—150)	(5—)6—9(—11) × 1.5—2.5(—3)	(2—)2.5—3.5(—4) × 2—3	Conidia distinctly truncate at base and relatively smooth-walled.
L. usneae	(40—)50—80(—100)	(5—)7—9(—11) × (2—)2.5—3.5(—4)	(2.5—)3—4(—5)	—
L. xanthoriae	(80—)100—175(—200)	(5—)6—8(—11) × (2—)2.5—4	(2.5—)3—4.5(—6)	—

arise from germinating conidia, several of which have been noted in the course of examining microtome sections. The conidia in *L. parasiticum* and *L. usneae* appear to germinate by the production of a somewhat swollen hyphal-like extension through the former point of attachment to the conidiogenous cell.

Lichenoconium species colonising already unhealthy tissues in particular, not infrequently occur together with other lichenicolous fungi including *Abrothallus curreyi* Linds. (with *L. cargillianum*), *A. parmeliarum* (Sommerf.) Arnold (with *L. usneae*), *A.* species (with *L. usneae*), *Arthonia clemens* (Tul.) Th. Fr. (with *L. parasiticum*), *Cornutispora lichenicola* D. Hawksw. & Sutton (with *L. usneae*), *Microdiplodia lecanorae* Vouaux (with *L. parasiticum*), *Phacopsis huuskonenii* Räs. (with *L. usneae*), *Phoma cytospora* (Vouaux) D. Hawksw. (with *L. parasiticum*), *P. physciicola* Keissl. (with *L. usneae*) and *P.* species (with *L. erodens*). Two *Lichenoconium* species may also occur in the same apothecium (e.g. *L. erodens* and *L. parasiticum* on *Parmelia galbina*, Pl. 24c; *L. usneae* and *L. xanthoriae* on *P. olivacea*).

GENERIC CONCEPTS

The generic name *Coniothyrium* Corda, lectotypified by *C. palmarum* Corda, was conserved in the 1956 Code but, as pointed out by Sutton (1971), *C. palmarum* has conidia which become finely punctate and 1-septate when mature and annellide-like conidiogenous cells (proliferating phialides) whereas Petrak & Sydow (1927) had based their concept of the genus on *C. fuckelii* Sacc. which has smooth and simple conidia borne on non-proliferating phialdes and for which the generic name *Microsphaeropsis* Höhn. can be used (Sutton, 1971). *Lichenoconium* thus appears to be generically distinct from both *Coniothyrium* s.s. and *Microsphaeropsis* on the basis of the simple conidia, and verruculose conidia on proliferating phialides, respectively. At least four species of *Coniothyrium* auct. do, however, have verrucose conidia (Hawksworth & Punithalingam, 1975) although in these the ornamentation is much coarser than that seen in *Lichenoconium* (see also the carbon replica electron micrographs of Punithalingam & Jones, 1970, which confirmed *C. fuckelii* as smooth-spored and showed the verrucose ornamentation in three species of *Coniothyrium* auct.); furthermore, these species are not known to produce proliferating phialides. At the present time there thus appears to be little problem in the separation of *Lichenoconium* (excl. *L. boreale* and *L. pertusariicola*) from other non-lichenicolous genera, but as more of the numerous non-lichenicolous species placed in *Coniothyrium* in the past are critically examined it is possible that problems in generic delimitation may arise. Morgan-Jones (1974), for example, did not consider conidial ornamention of value at the generic level and illustrated conidia of '*Microsphaeropsis*' *concentrica* (Desm.) Morgan-Jones by SEM which have verruculose ornamentation not unlike that seen in the lichenicolous species; that species is, however, reportedly strictly phialidic.

The generic distinctiveness of *L. boreale* and *L. pertusariicola* has already been mentioned (p. 160) and the characters separating them are discussed under those species in more detail.

LICHENOCONIUM Petr. & Syd.

Lichenoconium Petr. & Syd. *in* Beih. Repert. Spec. nov. Regni veg. **42**: 432. 1927. — Holotype: *Coniothyrium lichenicola* P. Karst. [syn. *L. lichenicola* (P. Karst.) Petr. & Syd.].

The following generic description excludes *L. boreale* and *L. pertusariicola* which are retained in *Lichenoconium* here only as an interim measure.

Pycnidia scattered to somewhat aggregated, immersed to erumpent or almost superficial when mature, subglobose to pyriform or cupuliform, black, lacking a clearly differentiated ostiole and opening by an often large irregularly formed pore; pycnidial wall composed of (1—)2—4(—6) layers of pseudoparenchymatous cells, cells polyhedral to rounded, sometimes laterally compressed, the outer rather thick-walled and dark brown, the inner thinner walled and generally hyaline. Conidiogenous cells lining the internal wall of the pycnidial cavity and extending up to the pore, formed in a single layer, phialidic or proliferating and annellide-like with 1—2 annellations, subcylindrical to ampulliform, hyaline throughout or becoming brownish and verruculose apically. Conidia arising singly from the apices of the conidiogenous cells, not adhering in chains, globose to pyriform or elongate-clavate, sometimes with a clearly differentiated truncate base, brown to dark brown singly but usually appearing black in mass, not distinctly guttulate, not septate, walls appearing almost smooth to coarsely verruculose or somewhat echinulate by light microscopy, in all species examined found to be verruculose or echinulate by SEM.

HOSTS.—As restricted above, known only from lichenized fungi of which they are parasites or saprophytes.

DISTRIBUTION.—Widespread in Europe but also known from Australasia, North America and Mexico.

NUMBER OF SPECIES.—Eight species definitely belonging to *Lichenoconium* are treated here together with two additional species retained in it 'ad interim'. The characters separating these ten species are summarised in the key below and in Table III.

KEY TO THE SPECIES OF *Lichenoconium*

1a. Pycnidial wall prosenplectenchymatous; pycnidia (100—)150—250 µm diam.; conidiogenous cells (8—)10—12 × 1—2(—2.5) µm; conidia almost hyaline to greenish-olivaceous, asymmetric-ellipsoid to almost reniform, (2.5—)3—3.5(—4) × 1.5—2.5 µm; on wood, Finland . . . . *L. boreale*, p. 171

b. Pycnidial wall pseudoparenchymatous; conidiogenous cells mainly exceeding 2 µm in width; conidia pale brown to dark brown; on lichens 2

2a. Outer layers of the pycnidial wall hyaline; pycnidia 100—250(—325) µm diam.; conidiogenous cells pale brown throughout, 3.5—10 × 2—3 µm; conidia mainly truncated-pyriform, smooth-walled, 3.5—6 × 2.5—3.5 µm; on thalli of *Pertusaria* species. *L. pertusariicola*, p. 182

b. Outer layers of the pycnidial wall dark brown; pycnidia less than 200 µm diam.; conidiogenous cells entirely hyaline or apically or basally pigmented; conidia echinulate or verrucose but in some species this is difficult to discerne by light microscopy. 3

3a. Pycnidia mainly exceeding 100 µm diam. 4

b. Pycnidia mainly less than 80 µm diam. 7

4a. Conidia (2—)2.5—3.5(—4) × 2—3 µm, rather smooth-walled; pycnidia (60—)80—120 (—150) × 50—80(—100) µm; on podetia and squamules of *Cladonia* species, Europe *L. pyxidatae*, p. 184

b. Conidia mainly exceeding 4 µm in length, distinctly verruculose 5

5a. Conidia tapered distinctly towards the truncated base, (4—)6—8(—9) × 3—4(—6) μm; pycnidia 100—200 μm diam.; conidiogenous cells (6—)8—13(—14) × 2—3.5 μm; on apothecia of *Physcia aipolia*, Finland . . . . *L. lichenicola*, p. 177
 b. Conidia globose to subglobose, sometimes rather angular 6
6a. Conidia (2.5—)3—4.5(—6) μm diam.; pycnidia (80—)100—175(—200) μm diam.; conidiogenous cells (5—)6—8 (—11) × (2—)2.5—4 μm; on apothecia (and rarely thallus) of *Cetraria sepincola*, *Parmelia olivacea* and particularly *Xanthoria* species, Europe *L. xanthoriae*, p. 190
 b. Conidia 5—7(—7.5) × 3.5—5(—6) μm; pycnidia 100—175(—200) μm diam.; conidiogenous cells (7—)8—10(—12) × (2.5—)3—3.5 μm; on apothecia of *Parmelia perforata* and apothecia and thalli of *Ramalina yemensis*, New Zealand and Mexico *L. cargillianum*, p. 172
7a. Pycnidia (20—)30—50(—60) μm diam.; conidiogenous cells (3.5—)4—5(—6) × (2—)3—3.5(—4) μm; conidia 2—3.5(—4) μm diam.; forming necrotic patches on the thalli and more rarely occurring in the apothecia of various lichens, Europe and U.S.A. *L. erodens*, p. 174
 b. Pycnidia mainly exceeding 50 μm diam.; conidia mainly exceeding 3.5 μm diam. . . . 8
8a. Conidiogenous cells (4—)5—7(—8) × (2—)3—3.5(—4) μm; conidia (2.5—)3—4.5 (—5.5) μm; pycnidia (30—)40—80(—100) μm diam.; on the thalli and in apothecia of various lichens, Europe and U.S.A. (If on *Pertusaria* see also under *L. erodens*.) *L. parasiticum*, p. 178
 b. Conidiogenous cells mainly exceeding 7 μm in height 9
9a. Conidia sparsely echinulate, 4.5—5 × 3—4 μm; pycnidia 65—125 μm diam.; conidiogenous cells (7—)8—10(—11) × 2—3 μm; on thalli of *Heterodea muelleri*, Australia *L. echinosporum*, p. 173
 b. Conidia verruculose, (2.5—)3—4(—5) μm diam.; pycnidia (40—)50—80(—100) μm diam.; conidiogenous cells (5—)7—9(—11) × (2—)2.5—3.5(—4) μm; on the thalli and in apothecia of various lichens, Europe . . . . *L. usneae*, p. 185

LICHENOCONIUM BOREALE (P. Karst.) Petr. & Syd.

Fig. 1A, Pl. 21A—E

Lichenoconium boreale (P. Karst.) Petr. & Syd. *in* Beih. Repert. Spec. nov. Regni veg. **42**: 436. 1927.—*Levieuxia borealis* P. Karst. *in* Hedwigia **26**: 126. 1887.—Holotype: Finland, Ostrobotnia australis; in Qvarken ad saepes, 15 July 1859, *P. A. Karsten* (H-Karst. 1493).

Pycnidia scattered, mainly superficial but immersed at the base to varying degrees, subglobose to almost cupuliform, black, (100—)150—250 μm diam., opening by an irregular pore; pycnidial wall 10—15 μm thick, composed of 3—8 irregular layers of almost prosenplectenchymatous hyphae; hyphae moderately thick-walled, mainly 3—3.5 μm wide, very variable in shape in vertical section, pale olivaceous brown but becoming even paler to hyaline at the conidiogenous cell layer. Conidiogenous cells lining the inner wall of the pycnidial cavity, holoblastic, phialidic or annellide-like with 1 annellation, cylindrical, not or only slightly swollen at the base, mainly hyaline but sometimes becoming brownish at the apex, (8—)10—12 × 1—2(—2.5) μm. Conidia arising singly from the apices of the conidiogenous cells, ellipsoid to pyriform, often somewhat allantoid, slightly truncated at the base, simple, at first almost colourless but maturing to pale olivaceous with a distinct greenish tinge within the pycnidial cavity, often 1—2 guttulate; walls appearing ± smooth by light microscopy but seen to have a close-packed verruculose ornamentation by SEM (×6000), (2.5—)3—3.5(—4) × 1.5—2.5 μm.

HOST.—On scarcely decomposed decorticate *Pinus* wood (lignum).
DISTRIBUTION.—Finland. Known only from the holotype collection from Replot on the northern island of Quarken in Ostrobotnia australis.
ETYMOLOGY.—From Latin *borealis*, northern.

This species, the only non-lichenicolous fungus treated in *Lichenoconium* here, differs from all the other accepted species in so many features that it ultimately will require transfer to another genus. The prosenplectenchymatous structure of the pycnidial wall, extremely slender conidiogenous cells, and the colour, shape, guttulation and ornamentation of the conidia, are the major differentiating features. As is the case with *L. pertusariicola*, *L. boreale* is retained in this genus pending a critical revision of generic concepts in the non-lichenicolous species of *Coniothyrium* Corda.

In view of its habitat, it is surprising that no further collections of this species appear to have been made. The scarcity of other fungi and little decomposition of the wood in the holotype material suggest that it occurred in a somewhat xeric situation.

Lichenoconium cargillianum (Linds.) D. Hawksw., *comb. nov.*

Fig. 1D, Pl. 25E—G

Microthelia cargilliana Linds. *in* Trans. R. Soc. Edinb. **24**: 439. 1866 (basionym). — Holotype: New Zealand, Otago, Saddlehill Bush, parasitic on *Parmelia perforata* on trunks of trees, [?2]5 Oct. 1861, *W. L. Lindsay* (E).

Coniothyrium ramalinae Vouaux *in* Bull. trimest. Soc. mycol. Fr. **30**: 296. 1914. — Holotype: Mexico, l'Etat de Puebla, Esperanza, alt. 2400 m, on *Ramalina yemensis*, 18 Nov. 1907, *M. Brouard* (hb. Vouaux).

Pycnidia scattered, immersed except near the apex or below and becoming erumpent, subglobose to almost cupuliform, black, 100—175(—200) µm diam., opening by an irregular pore or split and sometimes becoming expanded; pycnidial wall mainly 7—10 µm thick, composed of 2—4 layers of pseudoparenchymatous cells; cells polyhedral to rounded, the outer thick-walled and dark brown, the inner thinner walled and paler brown to subhyaline, mainly 4—10 µm diam. Conidiogenous cells lining the inner wall of the pycnidial cavity, phialidic or rarely annellide-like with 1 annellation, subcylindrical to ampulliform below, mainly hyaline but sometimes becoming slightly pigmented and verruculose apically, (7—)8—10(—12) × (2.5—)3—3.5 µm. Conidia arising singly from the apices of the conidiogenous cells, rather irregularly subglobose to almost pyriform, distinctly truncated at the base, dark brown but appearing almost black in mass, often with a single large guttule; walls appearing very coarsely verruculose by light microscopy, not examined by SEM, 5—7(—7.5) × 3.5—5(—6) µm.
HOSTS.—On *Parmelia perforata* Ach. (apothecia) and *Ramalina yemensis* (Ach.) Nyl. (apothecia and thallus).
DISTRIBUTION.—Mexico and New Zealand. Known only from the two collections cited above.
ETYMOLOGY.—Named in honour of John Cargill, F.R.G.S., a friend of Lindsay's, who was a pioneer settler in Otago and a member of the then Legislative Assembly in New Zealand (*fide* Lindsay, 1866).
ILLUSTRATIONS —Lindsay *in* Trans. R. Soc. Edinb. **24**: Pl. 30 figs. 31—34. 1866. — Hawksworth *in* Trans. Br. mycol. Soc. **67**: 55, fig. 3 A-B. 1976.

Lichenoconium cargillianum is separated from the other species of the genus with large (exceeding 100 µm diam.) pycnidia by its conidia which are extremely coarsely verrucose, subglobose and comparatively large. It is most similar to *L. lichenicola* but can be distinguished from that species by the generally shorter and differently shaped conidia.

In the case of the collection on *Parmelia perforata*, which has *Abrothallus curreyi* Linds. on its thallus (not the apothecia; this specimen is also the type collection of this *Abrothallus*), the apothecia are mainly superficial while in that on *Ramalina yemensis* they are largely immersed. For this reason I was for some time undecided whether to regard the fungi on these two hosts as specifically distinct, but in view of the variation in the degree of immersion of the pycnidia seen in some other species of the genus and the extremely close similarity in all other respects they can hardly be treated as separate on the basis of the information so far available.

Lichenoconium echinosporum D. Hawksw., *spec. nov.*

Fig. 1B, Pl. 22A—E

Pycnidia dispersa, immersa sed ad apices erumpescentia, subglobosa, nigra, 65—125 µm diam., dehiscentia ad porum irregulariter; muri pycnidii usque 7—10 µm crassi, e 2—4 stratis cellularum pseudoparenchymaticarum compositi, cellulis polyedricis vel rotundatis, 6—8(—10) µm diam., extra atrobrunneis et crassoparietalibus. Cellulae conidiogenae phialidicae, subcylindricae vel ampulliformes, plerumque hyalinae sed cum apicibus leviter pigmentifera, (7—)8—10(—11) × 2—3 µm. Conidia sublobosa ad irregulariter obpyriformis, basi leviter truncata, brunnea ad atrobrunnea, non distincte guttulata, minute parce echinulata, 4—5.5 × 3—4 µm.

Holotypus: Australia, New South Wales, proxime Waterfall National Park, circa 24 miles SW e Sydney, in thallo *Heterodeae muelleri* (Hampe) Nyl., 2. XI. 1954, *M. Tindale* (UPS).

Pycnidia scattered, immersed but becoming erumpent at the apices, subglobose, black, 65—125 µm diam., opening by an irregular pore; pycnidial wall mainly 7—10 µm thick but sometimes reaching 25 µm thick near the opening, composed of 2—4 layers of pseudoparenchymatous cells; cells polyhedral or becoming rounded, 6—8(—10) µm diam., the outer dark brown and thick-walled, the inner pale brown to subhyaline and thinner walled. Conidiogenous cells lining the internal wall of the pycnidial cavity, phialidic, no annellations seen, subcylindrical to ampulliform, mostly hyaline but with the apices often slightly pigmented, (7—)8—10(—11) × 2—3 µm. Conidia arising singly from the apices of the conidiogenous cells, subglobose to irregularly obpyriform, slightly truncated at the base, brown to dark brown, not distinctly guttulate, walls with a distinctive sparsely echinulate ornamentation best seen by SEM (×6000), 4—5.5 × 3—4 µm.

Holotype.—Australia, New South Wales, near Waterfall National Park, *c.* 24 miles south-west of Sydney, Hawkesbury sandstone scrub, on dry Hawkesbury sandstone rock face, on thallus of *Heterodea muelleri* (Hampe) Nyl., 2 Nov. 1954, *M. Tindale L10* (UPS).

Host.—*Heterodea muelleri* (Hampe) Nyl. (thallus).

Distribution.—Australia (New South Wales). Known only from the type collection.

Etymology.—From Latin *echinatus*, spiny and *spora*, spore.

This previously unrecognised species resembles *L. usneae* in the length of its conidiogenous cells but differs in that the conidia are ornamented with dispersed minute spine-like structures rather than compacted verrucae. In addition the pycnidia and conidia tend to be in the upper size ranges for these characters in *L. usneae*. No other *Lichenoconium* is known to me from this host or from Australia.

Lichenoconium echinosporum is certainly a pathogen rather than a parasymbiont, opportunist or saprophyte, as it attacks the normally greenish grey lobes discolouring them to pale brownish. At the interface between the infected patches and healthily growing lobes a darker brown zone mainly 70—100 µm wide develops; immediately outside this zone the lobes tend to assume a yellowish tinge. The pycnidia are scattered through the brownish patches which vary in extent and ultimately extend over the whole of the lobe.

Lichenoconium erodens M.S. Christ. & D. Hawksw., *spec. nov.*

Fig. 1C, Pls. 23A—F, 24A—D

Pycnidia dispersa, immersa sed ad apices erumpescentia, subglobosa, nigra, (20—)30—50(—60) µm diam., dehiscentia ad porum irregulariter; muri pycnidii usque 3.5—7 µm crassi, e 1—3 stratis cellularum pseudoparenchymaticarum compositi, cellulis polyedricis vel rotundatis, plerumque 3—5 µm diam., atrobrunneis et crassoparietalibus. Cellulae conidiogenae phialidicae, brevisubcylindricae vel ampulliformes, plusminusve hyalinae, (3.5—)4—5(—6) × (2—)3—3.5(—4) µm. Conidia subglobosa, brunnea, non distincte guttulata, verruculosa, 2—3.5(—4) µm diam.

HOLOTYPUS: Suecica, Scania, Hallands Väderö, in thallo *Hypogymniae physodis* (L.) Nyl., 27.VIII.1971, *M. Skytte Christiansen* (hb. Christiansen 61).

Pycnidia scattered, immersed but becoming erumpent at the apices, subglobose, black, (20—)30—50(—60) µm diam., very exceptionally to 75 µm wide, opening by an irregular pore; pycnidial wall mainly 3.5—7 µm thick, composed of 1—3 layers of pseudoparenchymatous cells; cells polyhedral to rounded, mainly 3—5 µm diam., dark brown and thick-walled. Conidiogenous cells lining the internal wall of the pycnidial cavity, phialidic or annellide-like with 1 annellation, short subcylindrical to ampulliform, more or less hyaline throughout, (3.5—)4—5(—6) × (2—)3—3.5(—4) µm, very exceptionally (on *Pertusaria*) to 8 µm tall. Conidia arising singly from the apices of the conidiogenous cells, subglobose, rather regular in shape, not markedly truncated at the base, brown, not distinctly guttulate; walls distinctly verruculose by light microscopy and SEM (×6000), 2—3.5(—4) µm diam.

HOLOTYPE.—Sweden, Scania, Hallands Väderö, *Prunus spinosa* in a copse near the sea shore, on thallus of *Hypogymnia physodes* (L.) Nyl., 27 August 1971, *M. Skytte Christiansen* (hb. Christiansen 61; isotype: hb. Christiansen 62).

HOSTS.—On *Evernia prunastri* (L.) Ach. (thallus), *Hypogymnia bitteriana* (Zahlbr.) Krog (thallus), *H. physodes* (L.) Nyl. (thallus), *Lecanora chlarona* (Ach.) Nyl. (apothecia), *Parmelia galbina* Ach. (syn. *P. subquercifolia* Hue; apothecia), *P. perlata* (Huds.) Ach. (thallus), *P. saxatilis* (L.) Ach. (thallus), *Parmeliopsis ambigua* (Wulf.) Nyl. (thallus), *Pertusaria hymenea* (Ach.) Schaer., and *P. pertusa* (L.) Tuck.

DISTRIBUTION.—Austria, British Isles, Denmark, France, Germany, Sweden, and the U.S.A. (New Jersey).

ETYMOLOGY.—From Latin *erosus*, eroded, after the irregularly margined holes this fungus produces in the thallus of *Hypogymnia physodes* in particular.

OTHER SPECIMENS EXAMINED.—On *Evernia prunastri*: BRITISH ISLES: Scotland, Angus, Montrose, 1857, [collector unknown] (E, IMI 205336); East Perth, Blaeberry Hill, March 1856, *W. L. Lindsay* (E); West Perth, Perth, Kinnoull Hill, April 1856, *W. L. Lindsay* (E); East Ross, Bayfield Loch, Nigg Hill, on pine bark, 1 Aug. 1968, *J. T. Swarbrick* (E). — DENMARK: South Jutland, Løgumkloster, Draved, on oak in the wood 'Draved Skov', 1 June 1973, *M. Skytte Christiansen* (hb. Christiansen 77).

On *Hypogymnia bitteriana*: AUSTRIA: Kärnten, Reisach im Gailtal, Schönboden, on north facing side of *Picea abies* in wood on south slope of Gailtal Alps, alt. 850—950 m. 10 July 1976, *M. Skytte Christiansen 76.542* (hb. Christiansen 114, 115).

On *Hypogymnia physodes*: BRITISH ISLES: England, South Devon, Chudleigh, Ugbrooke Park, on *Quercus*, 31 Aug. 1976, *D. L. Hawksworth 4350* (IMI 206392*a*). — DENMARK: North Jutland, Tværsted, on oaks in a dune plantation, 5 Oct. 1968, *M. Skytte Christiansen* (hb. Christiansen 63); South Jutland, Løgumkloster, Draved, on *Salix aurita* in a birch bog in the eastern part of the wood 'Draved Skov', 27 March 1975, *M. Skytte Christiansen 75.408* (hb. Christiansen 72, 73, 74, 75). — GERMANY: Bayerisch-Böhemischer Wald, Niederbayern, Plenterartig bewirtschafteter tanneneichen Mischwald westlich-NW Grainet, Kreis Wolfstein, 700—730 m, 8 Sept. 1971, *J. Poelt* (hb. Poelt 10401). — SWEDEN: Västergötland, Kindaholm, Mårdaklev, on *Sorbus aucuparia* in a spruce forest, 30 March 1975, *M. Skytte Christiansen 75.024* (hb. Christiansen 60, 69, 71).

On *Lecanora chlarona*: BRITISH ISLES: Scotland, Selkirk, Bowhill, on fence rail, 25 Sept. 1976, *B. J. Coppins 2377* (E).

On *Parmelia galbina*: U.S.A.: New Jersey, Lebanon St. Forest, Burlington Co., 1 Sept. 1957, *M. E. Hale 15246b* (UPS; with *L. parasiticum*).

On *Parmelia perlata*: FRANCE: Dept. Dordogne, Sarlat, on oak in a wood near the camping site 'Le Roch', alt. 140 m, 17 July 1973, *M. Skytte Christiansen* (hb. Christiansen 102).

On *Parmelia saxatilis*: DENMARK: South Jutland, Løgumkloster, on young oak in the wood 'Draved Skov', 21 May 1976, *M. Skytte Christiansen 76.097* (IMI 205333; hb. Christiansen).

On *Parmeliopsis ambigua*: AUSTRIA: Grazer Bergland, Steiermark, Hänge der Breitelmhalb auf der Teichalpe, 1150—1350 m, Aug. 1973, *J. Poelt* (hb. Poelt).

On *Pertusaria hymenea*: BRITISH ISLES: England, East Sussex, Brede, Little Parkwood, on *Quercus*, 7 March 1973, *B. J. Coppins* (E; IMI 189795).

On *Pertusaria pertusa*: DENMARK: South Jutland, Løgumkloster, on oak in the wood 'Draved Skov', 12 Sept. 1973, *M. Skytte Christiansen* (hb. Christiansen 99, 107 p.p.); Zealand, Søllerød, Strandmøllen, on *Fraxinus*, 26 March 1945, *M. Skytte Christiansen* (hb. Christiansen 98).

Lichenoconium erodens is most similar to *L. parasiticum*, from which it differs in the generally much smaller pycnidia, somewhat shorter conidiogenous cells and characteristically small conidia. The conidia recall those of *L. pyxidatae* in size but differ in being more verruculose and not markedly truncated at the base; *L. pyxidatae* has much larger pycnidia and conidiogenous cells but the similarity in conidial size may have led some specimens of *L. erodens* to be referred to *L. pyxidatae* in the past.

Although *L. erodens* might perhaps be viewed as a diminutive *L. parasiticum*, it appears to merit separation at the species level in view of (i) the several differentiating anatomical features, (ii) the ability of it to form dissimilar symptoms to those produced by *L. parasiticum* on the same host (see p. 166), and (iii) its occurrence in mixed infections with *L. parasiticum* where it maintains its identity. In practice the separation of these two species seems to present little difficulty.

In *Evernia prunastri* infection occurs generally in the distal branches and tips where the cortex is not yet fully developed but has also been found in some specimens in perhaps already unhealthy median and basal parts of the thallus. The pycnidia predominate in the upper cortex but also may occur in the soralia and on lobe tips; in one instance a pycnidium occurred on the underside of a lobe but this seems uncharacteristic. The infected parts of the thallus become discoloured brownish by the time the pycnidia are visible and in general the boundary between diseased and healthy tissue is diffuse and not marked by a black border (Pl. 23E); in one specimen with a mixed infection including a *Phoma* species (*Swarbrick*, E) a border to 250 µm wide, however, occurred.

The infection spots in *Hypogymnia physodes*, in contrast, almost always have a well-defined blackened border, often 100—200 µm wide; the only exception to this appears to be in particularly diseased thalli (often in the presence of other lichenicolous fungi) when the host is unable to respond to the infection by producing the brown and thick-walled hyphae which constitute the border zone. Within the spots, which may be brownish grey to pale grey or almost whitish, the cortex is almost normal in structure when the pycnidia are first discernible but this becomes degenerate as the pycnidia mature and finally breaks down completely; the result of this is that the central part of the infection spot tends to fall out and leave a black-bordered irregularly margined hole in the thallus (Pl. 23A—C). Several pycnidia are almost always to be found within the same spot which is most often about 0.5—2 mm diam. Where a thallus is also attacked by another fungus, such as a *Phoma* species (which is not uncommon), its fruits tend to be confined to different, although superficially similar, infection spots although occasionally fruits of different fungi can occur in the same spot (e.g. Pl. 23 D and *Christiansen 75.024*). The symptoms which this fungus produces in *Hypogymnia bitteriana*, *Parmelia perlata* and *P. saxatilis* are similar to those in *H. physodes* and have several pycnidia in each spot; the degree of development of the border in *H. bitteriana* and *P. saxatilis* seems rather more variable, however. The above observations clearly indicate that *L. erodens* is a pathogen of these species and *Evernia prunastri*.

In the case of infections in *Lecanora chlarona* and *Parmelia galbina*, the pycnidia are restricted to the apothecia and may occupy the whole height of the thecial tissues. Although ascospore production may be reduced by their presence, the only visible symptoms of damage are the discs of the apothecia becoming blackened due to both the presence of the pycnidia themselves and the conidia discharged onto the surface of the epithecium. These symptoms are similar to infections of apothecia by other species of *Lichenoconium* (e.g. *L. parasiticum*, *L. usneae*).

In the case of infections of *Pertusaria pertusa* thalli the pathogenic tendencies are again evident with the production of extensive discoloured areas. Material on *P. hymenea* was too scant to assess the extent to which it is harmful to that host. The three collections on *Pertusaria* cited above are placed here with some hesitation and were first referred to *L. parasiticum* despite their rather small conidia ((2)—2.5—3.5(—4) µm diam.) because of the pycnidia which are rather large for *L. erodens* (to 75 µm wide). In view of these considerations, the disparate hosts, and also the tendency for the conidiogenous cells to be larger than is usual in *L. erodens* (4—6(—8) × 3—4 µm) it is possible that these represent an undescribed species. In the absence of further collections, however, I feel it would be premature to describe them as such here.

LICHENOCONIUM LICHENICOLA (P. Karst.) Petr. & Syd.

Fig. 1E, Pl. 25A—D

Lichenoconium lichenicola (P. Karst.) Petr. & Syd. *in* Beih. Repert. Spec. nov. Regni veg. **42**: 432. 1927. — *Coniothyrium lichenicola* P. Karst. *in* Meddn Soc. Fauna Flora fenn. **14**: 104. 1887 [as '*lichenicolum*']. — Holotype: Finland, Tavastia australis (Ta), Lahtis (Lahti), [on *Physcia aipolia*], 27 March 1872, *P. A. Karsten* (H-Karst. 1246).

Pycnidia scattered, immersed below but markedly erumpent above when mature, subglobose, black, 100—200 µm diam., opening by a large irregular pore; pycnidial wall mainly 7—12(—15) µm thick, occasionally to 20 µm thick near the opening, composed of (1—)2—4 layers of pseudoparenchymatous cells; cells polyhedral, thick-walled, mainly 5—10 × 4—7 µm, the outer dark brown to almost black, the inner brown to almost hyaline. Conidiogenous cells lining the internal wall of the pycnidial cavity, annellide-like with (0—)1—2(—3) annellations, subcylindrical to somewhat ampulliform, mainly hyaline but becoming slightly to moderately pigmented and verrucose both apically and basally, (6—)8—13(—14) × 2—3.5 µm. Conidia arising singly from the apices of the conidiogenous cells, very variable in shape, subglobose to ellipsoid or clavate, distinctly tapered and truncated at the base, brown to dark brown, not distinctly guttulate; walls appearing coarsely verrucose by light microscopy and SEM (× 6000), (4—)6—8(—9) × 3—4(—6) µm.

HOSTS.—On *Physcia aipolia* (Ehrh. ex Humb.) Hampe (apothecia). The host was incorrectly assigned to the genus *Parmelia* Ach. by Karsten (1887) who was followed, for example, by Keissler (1910, 1930), Vouaux (1914) and Petrak and Sydow (1927). The reference to the occurrence of this species on *Physcia adscendens* (Th.Fr.) Oliv. (syn. *P. ascendens* Bitt.) in France by Vouaux (1914) requires confirmation; unfortunately the specimen supporting that record is lost but the conidial measurements given (5—7 × 2.5—3.5 µm) suggest *L. lichenicola*. Keissler's (1930) mention of the species from *Xanthoria parietina* in France is almost certainly an error for *L. xanthoriae*. The var. *buelliae* (Keissl.) Keissl., reported from *Buellia disciformis* and *Pertusaria* species, does not belong to *L. lichenicola* and is discussed separately below (p. 182).

DISTRIBUTION.—Known with certainty only from the holotype collection made in Finland.

ETYMOLOGY.—From Greek Λειχήν, lichen, and Latin *-icola*, dweller.

ILLUSTRATIONS.—Hawksworth *in* Trans. Br. mycol. Soc. **65**: 232 fig. 4 E-F. 1975.

The apothecia in the holotype collection are heavily infected with pycnidia. These are mainly localised in the apothecial discs themselves but some were also observed on the thalline margin under the edge of the apothecium. The surface of the disc is normally black in *Physcia aipolia* and so does not change in colour when infected, although it tends to appear duller than is usual in healthy material of this species.

Within the thecium the asci present are mainly older ones and the ascospores within them often deformed. Dark brown hyphae of the parasite, somewhat torulose in appearance, with slightly verruculose walls and 3—4(—5) µm wide, may be seen in section to pass from the outer cells of the pycnidial wall into the hypothecium; similar hyphae also spread out to a limited extent on the surface of the epithecium around the pycnidia.

Lichenoconium lichenicola is readily separable from all other species of the genus. Not only are the conidiogenous cells larger than in any other species of it, but the coarsely verrucose conidia are larger and characteristically shaped. Clavate conidia still attached to conidiogenous cells are occasionally seen in many species of the genus with smaller pycnidia, conidiogenous cells and conidia (e.g. *L. usneae*, which can also occur on *Physcia aipolia*) and generally seem either to be very young or ones which have continued to grow having failed to secede at the dimensions usual in the species. In *L. lichenicola*, however, the conidia occur free both within the pycnidial cavity and on the surface of infected apothecia and so cannot be regarded as abnormal productions.

Lichenoconium parasiticum D. Hawksw., *spec. nov.*

Fig. 1F, Pls. 26A—G, 27 A—D

Lichen stictoceros Sm. *in* Smith & Sowerby, Engl. Bot. **19**: tab. 1353. 1804 pro parte; nom. illegit. (Art. 70). — Holotype: British Isles, England, South Devon, 'in the warren opposite to Exmouth intermixed with a lichen like the *articulatus*', 29 April 1803, *J. Brodie* (E); isotype: IMI 205337. — For further obligate synonyms see Zahlbruckner, Cat. Lich. Univ. **6**: 360—361. 1930.

Lichenoconium lecanoracearum sensu Petr. & Syd. *in* Beih. Repert. Spec. nov. Regni veg. **42**: 434. 1927.

Pycnidia dispersa vel laxe aggregata, immersa sed ad apices erumpescentia, subglobosa vel ovoidea, nigra, (30—)40—80(—100) µm diam., dehiscentia ad porum irregulariter; muri pycnidii usque (3—)5—7(—10) µm crassi, e 2—4(—5) stratis cellularum pseudoparenchymaticarum compositi, cellulis polyedricis vel rotundatis, plerumque (3—)5—7 µm diam., atrobrunneis et crassoparietalibus. Cellulae conidiogenae phialidicae vel annellidicae, brevisubcylindricae vel ampulliformes, plusminusve hyalinae, (4—)5—7(—8) × (2—)3—3.5(—4) µm. Conidia subglobosa, brunnea, non distincte guttulata, verruculosa, (2.5—)3—4.5(—5.5) µm diam.

HOLOTYPUS: Dania, Sjælland, Herstedvester, Vridsløselille, in apotheciis *Lecanoræ conizaeoidis* Nyl. ex Cromb., 20.VII.1944, *M. Skytte Christiansen* (hb. Christiansen 97).

Pycnidia scattered or loosely aggregated into small groups, immersed but becoming erumpent above, subglobose to ovoid, black, (30—)40—80(—100) µm diam., opening by an irregular pore; pycnidial walls mainly (3—)5—7(—10) µm thick, composed of 2—4(—5) layers of pseudoparenchymatous cells, cells polyhedral to rounded, mainly (3—)5—7 µm diam., the outer dark brown and thick walled, the inner pale brown to subhyaline and thinner walled. Conidiogenous cells lining the internal wall of the pycnidial cavity, phialidic or annellide-like with 1(—2) annellations, more or less hyaline throughout but occasionally becoming slightly pigmented and verruculose apically, (4—)5—7(—8) × (2—)3—3.5(—4) µm. Conidia subglobose, usually rather regular in shape, only occasionally clearly truncate at the base, brown to dark brown, not distinctly guttulate, walls distinctly verruculose by light microscopy and SEM (×6000), (2.5—)3—4.5(—5.5) μm diam.

HOLOTYPE.—Denmark, Sjaelland, Herstedvester, Vridsløselille, on lignum, in apothecia of *Lecanora conizaeoides* Nyl. ex Cromb., 20 July 1944, *M. Skytte Christiansen* (hb. Christiansen 97; isotype —UPS).

HOSTS.—On thalli and (or) apothecia of numerous lichens including *Evernia prunastri* (L.) Ach., *Lecanora admontensis* Zahlbr., *L. chlarotera* Nyl. (syn. *L. rugosa* Nyl.), *L. conizaeoides* Nyl. ex Cromb. (syn. *L. pityrea* Erichs., *L. varia* auct. p.p.), *L. pallida* (Schreb.) Rabenh., *L. polytropa* (Hoffm.) Rabenh., *L. rubina* (Vill.) Ach. (syn. *L. chrysoleuca* (Sm.) Ach.), *L. subcarnea* (Liljebl.) Ach., *L. subfusca* (L.) Ach. aggr., *L. subfuscata* Magnusson, *L. superfluens* Magnusson, *Parmelia borreri* (Sm.) Turn., *P. pastillifera* (Harm.) Schub. & Klem., *P. saxatilis* (L.) Ach., *P. sulcata* Tayl., *P. galbina* Ach. (syn. *P. subquercifolia* Hue), and *Squamarina lentigera* (Web.) Poelt. Also reported, as *Coniothyrium lecanoracearum*, by Vouaux (1914) from *Bacidia rubella* (Hoffm.) Massal. (almost certainly an error; see p. 165), *L. concolor* Ram. (syn. *Squamaria concolor* var. *angusta* (Arnold) Oliv.), *L. intumescens* (Rebent.) Rabenh., *L. nitens* Ach., *L. pacifica* Tuck. (an error for *L. usneae*; see p. 190), and *L. symmictera* (Hepp) Nyl.; these reports cannot be checked in the absence of material in Vouaux's herbarium (Rondon, 1969) and as that formerly in Bouly de Lesdain's herbarium was destroyed in World War II.

DISTRIBUTION.—Austria, Belgium (Vouaux, 1914; in need of confirmation), British Isles, Canada, Czechoslovakia, Denmark, France, Germany, Hungary, Spain, Sweden, Switzerland and the U.S.A. (New Jersey).

ETYMOLOGY.—From Latin *parasiticus*, parasitic, after the parasitic tendencies often shown by this species.

EXSICCATAE.—Krypt. Exs. Vindob. no. 3282 (sub *Lichenoconium lecanoracearum*; IMI 12680, K, M).

OTHER SPECIMENS EXAMINED.—On *Evernia prunastri* (thallus): SWEDEN: Uppland, Vänge s:n, Jobso, nära Iv., på *Ulmus*, 15 Jan. 1961, *I. Nordin 133c* (UPS).

On *Lecanora admontensis* (apothecia): CZECHOSLOVAKIA: Tatra Magna, Belanské Tatry, in alpe 'Jatky', alt. 1950 m, Aug. 1964, A. *Vezda* (UPS; hb. Vezda).

On *Lecanora chlarotera* (apothecia): DENMARK: South Jutland, Løgumkloster, on *Quercus* in the wood 'Draved Skov', 12 Sept. 1973, *M. Skytte Christiansen* (hb. Christiansen 107 p.p.).

On *Lecanora conizaeoides* (apothecia; selected localities only listed): BRITISH ISLES: England, Norfolk, West Somerton, 9 March 1975, *F. S. Dobson* (IMI 192264): Norfolk, near Marthan, on *Alnus*, 22 April 1972, *F. S. Dobson* (IMI 202895); Northumberland, Newcastle upon Tyne, 1965, *O. L. Gilbert* (IMI 115841; see also Gilbert, 1966); Staffordshire, Wildboarclough, on *Acer pseudoplatanus*, 24 Oct. 1975, *D. L. Hawksworth 4214* (IMI 197748); Scotland, Fifeshire, Devillater, 9 March 1976, *B. J. Coppins* (E). — DENMARK: Jylland, Agri, Mols Bjærge, on wood of oak fencepost in heather moor, 15 Aug. 1945, *M. Skytte Christiansen 12796* (UPS). — GERMANY: Schleswig-Holstein, Kreis Lauenburg, ad corticem *Pini* proxime Lehmrade, Sept., *C. F. E. Erichsen*, Krypt. Exs. Vindob. no. 3282 (IMI 12680; K; M); Schleswig-Holstein, Hamburg, an *Alnus* im Gehölze u. Borstler Jäger, 21 Oct. 1927, *C. F. E. Erichsen 198* (UPS). — NETHERLANDS: Utrecht Prov., Baarn, roadside tree, 4 Nov. 1976, *D. L. Hawksworth 4370* (IMI 208602).

On *Lecanora* aff. *pallida* (apothecia): CZECHOSLOVAKIA: Moravia, prope opp. Velká Bítes, alt. 450 m, August 1963, *A. Vezda* (UPS; hb. Vezda). — GERMANY: Leipzig, 6 March 1876, *G. Winter* (M).

On *Lecanora polytropa* (apothecia): SWEDEN: Jämtland, Åre parish, Ånn, on ocks at the lake Ånnsjön, alt. 525 m, 22 Feb. 1957, *R. Santesson 11684* (UPS).

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On *Lecanora rubina* (apothecia and thallus): SWEDEN: Lapponiae Lulensis, in praeruptis parietibus alpis Rittock, 1871, *P. J. & E. V. M. Hellbom* (UPS). — SWITZERLAND: Wallis, La forclaz, on perpendicular rock face, alt. 1500 m, 13 July 1972, *M. Skytte Christiansen* (hb. Christiansen 108).

On *Lecanora subcarnea* (apothecia): SWEDEN: Västergötland, par. Partille, Surketjärn, 30 Sept. 1951, *A. H. Magnusson 22666* (UPS).

On *Lecanora subfusca* aggr. (apothecia): AUSTRIA: Grazer Bergland, Steiermark, Öbstbäume am Fahrweg zum Linecker nördlich okerhalb Wenisbuch, Bezirk Graz-Land, June 1972, *J. Poelt p.p.* (hb. Poelt 11319; with *Microdiplodia lecanorae*). — CZECHOSLOVAKIA: Carpati, montes Liptovské hole, *Sorbus aucuparia* in m. Suchý hrádok, alt. 1500 m, Aug. 1963, *A. Vezda* (hb. Vezda).

On *Lecanora subfuscata* (apothecia): SPAIN: Prov. Alava, near Peña de Oqueta (*c.* 18 km n.n.w. of Vitoria), alt. 650 m, *Quercus robur*, 8 May 1959, *R. Santesson 13273g* (UPS; see also Santesson, 1960).

On *Lecanora superfluens* (apothecia): CANADA: North West Territories, Baffin Island, head of Clyde Fiord, on wet soil near a large boulder, 26 June 1950, *M. E. Hale 4166 p.p.* (UPS; holotype of the host lichen; see also Magnusson, 1952).

On *Parmelia borreri* (thallus): BRITISH ISLES: England, Hampshire, West Meon, south of Chappets Farm, on *Fraxinus*, 17 Oct. 1972, *B. J. Coppins* (IMI 192265).

On *Parmelia galbina* (apothecia): U.S.A.: New Jersey, Lebanon State Forest, Burlington Co., 1 Sept. 1957, *M. E. Hale 15246b* (UPS; with *L. erodens*).

On *Parmelia pastillifera* (thallus): BRITISH ISLES: England, East Kent, Wye, s.-w. of station, on *Fraxinus*, 1967, *F. Rose* (IMI 208397).

On *Parmelia saxatilis* (thallus): DENMARK: Zealand, Dråby, on boulders facing n.e. in a stone-wall around the forest Nordskoven, near Kulhus, 28 Oct. 1942, *M. Skytte Christiansen 9798* (hb. Christiansen 104, 105; IMI 202905); Zealand, Haslev, in the park of the manor house Bregentved, on *Aesculus*, 2 Oct. 1975, *M. Skytte Christiansen 75.429* (hb. Christiansen 109).

On *Parmelia sulcata* (thallus and soralia): DENMARK: Zealand, Aagerup parish, on *Aesculus hippocastanum* in an avenue near the manor house Eriksholm, 25 Aug. 1941, *M. Skytte Christiansen 7582* (hb. Christiansen 16, 17); Zealand, Aarby parish, on *Ulmus* along the road from Lerchenborg to Asnaes Forskov, 8 Aug. 1944, *M. Skytte Christiansen* (hb. Christiansen 18, 19, 20); North Jutland, Skagen, Hulsig Krat, on *Populus tremula* in a small oak-scrub, 5 Oct. 1968, *M. Skytte Christiansen* (hb. Christiansen 21).

On *Squamarina lentigera* (apothecia): HUNGARY: Balaton, Tihany, 17 Aug. 1964, *A. Vezda* (hb. Vezda). — SWEDEN: Öland, Tveta ås, 20 June 1867, *J. E. Zetterstedt* (UPS).

Lichenoconium parasiticum is one of the commonest species of the genus and has a wide host range. When occurring in the apothecia of *Lecanora* and *Squamarina* species the apothecial discs are in general at first little affected by the presence of the pycnidia; in some instances, however, they are paler in colour than is usual as occurs in infections by *Vouauxiella* species. In the case of older infections of normally rather pale-fruited species, the infected discs tend to become entirely black; this reaction is particularly noticeable in *Lecanora conizaeoides* (Pl. 26A) where the blackened discs are an important field character for the recognition of this fungus. The black layer is due to both dark hyphae of the fungus growing over the disc, dispersed conidia, and the colour of the pycnidia themselves. In the case of infections on crustose or squamulose (placodioid) lichens, any indications of damage are normally restricted to the apothecia themselves but in the case of infections in *Lecanora admontensis* decolourised, somewhat bleached, lesions appear.

As interpreted here, *Lichenoconium parasiticum* is somewhat variable with respect to the sizes of the pycnidia and conidia when on different hosts (see Table IV) but, in view of the varying numbers of specimens available on different hosts, this may well be an artifact and is not considered taxonomically significant, particularly in view of the development of similar symptoms on, for example, *Parmelia* thalli. The three collections of *Lichenoconium* on *Pertusaria* with small globose conidia and pycnidia placed under *L. erodens* in this paper, were first referred to *L. parasiticum* in view of the pycnidia tending to be rather larger than is usual in *L. erodens*; the possibility that these may represent an undescribed species is discussed under *L. erodens*. The conidia in the collection on *Lecanora* aff. *chlarotera* (hb. Christiansen 107) had rather small conidia (2·5—3·5 µm diam.) and so may also belong to *L. erodens* but the material was too scant to enable this material to be studied in more detail.

One of the infected collections of *Lecanora rubina*' (hb. Christiansen 108) has a characteristic delicate brown network of hyphae developed over the surface of the host (Pl. 26D); as this network, amongst which pycnidia are scattered, is mainly restricted to the older parts of the thallus in this collection, is not found on a different collection on this same host (UPS), and as the pycnidial and conidial characters fall within the range of variation of *Lichenoconium parasiticum*, it is not treated as specifically distinct here.

When infections are established on the thalli of *Parmelia* species, individual pycnidia seem to almost invariably become restricted by black-bordered infection spots generally under 500 µm, but sometimes to 1 mm diam.; the dark border is rather

TABLE IV

LICHENOCONIUM PARASITICUM: VARIATION OF SELECTED CHARACTERS ON DIFFERENT HOSTS

Host	Pycnidia (µm diam.)	Phialides (µm)	Conidia (µm)
Evernia prunastri	30—60(—75)	6—7 × 2—3—3·5	3·5—5 × 2·5—3·5
Lecanora admontensis	50—80	5—7 × 3—3·5	3—4
L. conizaeoides	(25—)40—70(—75)	5—7 × (2·5—)3—3·5(—4)	3·5—4·5(—5·5)
L. pallida	50—80	5—7 × 2—3	(2·5—)3·5—4(—5)
L. rubina	(40—)50—70(—80)	4—6 × 3—4	(2·5—)3—4(—5)
L. subcarnea	50—80	few seen	3—4
L. subfusca aggr.	50—80	5—7 × 3·5—4	(3—)3·5—4(—4·5)
L. superfluens	50—75	4—5 × 3—3·5	3—4
Parmelia borreri	30—60	4—6 × 3—3·5	3—4·5(—5)
P. galbina	50—70	5—8 × 3—3·5	(3·5—)4—5(—5·5)
P. pastillifera	60—80	4—7 × 3—3·5	3·5—4
P. saxatilis	50—80	4—6 × 3—3·5	3—4 × 3—3·5
P. sulcata	40—60(—70)	5—7 × 3—3·5	3—3·5(—4)
Squamarina lentigera	(50—)70—90(—100)	4—8 × 3—3·5	(2·5)—3·5—4(—4·5)

variable in thickness but generally 50—150 µm wide. Spots may coalesce in heavily infected thalli to give the whole a mottled appearance. The host tissue within the spots becomes pale brownish but usually persists, unlike infections of *Parmelia* thalli by *L. erodens*, which also differ in generally having several pycnidia in each infection spot. The area within the spot often has a thinner cortex than usual (e.g. 5—10 µm not 15—20 µm thick). The separation of *L. erodens* and *L. parasiticum* has already been referred to and their distinctness is considered to be supported by their joint occurrence in the apothecia of *Parmelia galbina* (Pl. 24C—E).

The epithet '*lecanoracearum*' was applied to this species by Petrak & Sydow (1927) who studied material on *Lecanora conizaeoides*; Vouaux (1914) had, however, applied this name to a mixture of species and an isosyntype proved to be *L. usneae*. It was also very poorly understood by Keissler (1930), to judge from his description which, for example, gave the conidia as only 2—3 µm diam. Because of these confusions (see also p. 190) the new name *L. parasiticum* is proposed here.

Lichenoconium usneae, which closely resembles *L. parasiticum* in its pycnidial and conidial sizes, is separated from *L. parasiticum* principally on the basis of the consistantly longer conidiogenous cells which are mainly in the range 7—9 µm tall. That this difference is taxonomically important at the species level is supported by the rather different host ranges involved, and the generally less severe damage caused when it occurs on the same host species (see Table IV); these considerations indicate that the taxa also have some degree of physiologic (biologic) separation in addition to this anatomical difference.

LICHENOCONIUM PERTUSARIICOLA (Nyl.) D. Hawksw.

Fig. 2A, Pl. 29A—C

Lichenoconium pertusariicola (Nyl.) D. Hawksw. *in* Trans. Br. mycol. Soc. **65**: 233. 1975. — *Spilomium pertusariicola* Nyl. *in* Mém. Soc. Imp. Sci. nat. Cherbourg **5**: 91. 1858; as '*pertusaricola*'. — *Coniothecium pertusariicola* (Nyl.) Keissl. *in* Rabenh. Krypt.-Fl. **8**: 620. 1930. — Holotype: France, in sylvae Fontainebleau, [on *Pertusaria pertusa*] ad *Fagus*, *W. Nylander* (H-Nyl. 23576).

? *Spilomium leioplacae* Oliv. *in* Bull. Acad. int. Géogr. bot. **17**: 176. 1907. — Holotype: not located.

Coniothyrium lichenicola var. *buelliae* Keissl. *in* Zentbl. Bakt. ParasitKde, Abt. II, **27**: 209. 1910. — *Lichenoconium lichenicola* var. *buelliae* (Keissl.) Keissl. *in* Rabenh. Krypt.-Fl. **8**: 560. 1930. — Holotype: Germany, Thüring Wald, Gehlberg, 650 m, auf d. thallus v. *Buellia disciformis* [?], June 1908, *G. Lettau* (W).

Pycnidia scattered to somewhat aggregated, immersed to erumpent, subglobose to globose or elongate-pyriform, black, rather invariable in size, mainly 100—250 (—325) µm diam.; pycnidial wall 5—20 µm thick, composed of 2—3(—4) layers of pseudoparenchymatous cells; cells polyhedral to rounded, thin-walled, mainly 3.5—8 µm diam., the outer ± hyaline, the inner pale brown to brown. Conidiogenous cells lining the internal wall of the pycnidial cavity, annellide-like with 1—2 annellations, subcylindrical to elongate-ampulliform, fuscous brown to brown (not hyaline) and smooth-walled throughout, 3.5—10 × 2—3 µm. Conidia arising singly from the apices of the conidiogenous cells, subglobose to ellipsoid, markedly truncated at the base, pale brown singly but appearing almost black in mass, not distinctly guttulate, smooth-walled even by SEM (×8000), 3.5—6×2.5—3.5 µm.

HOSTS.—On thalli of *Pertusaria leioplaca* (Ach.) DC. and *P. pertusa* (L.) Tuck. It may also occur on the thalli of *P. texana* Müll. Arg. to judge from the illustrations of Dibben (1974, figs. 123—4, sub *Coniothecium* sp.). References to its occurrence on the thallus of *Buellia disciformis* (Fr.) Mudd are treated as dubious; the holotype of var. *buelliae* is now only represented by a slide of the fungus and the identity of the host cannot be verified from it (Hawksworth, 1975).

DISTRIBUTION.—British Isles, Denmark, France, Germany, Ireland and Spain. It may also occur in North America if Dibben's (1974) *Coniothecium* sp. proves to belong here. In Denmark it is most often found in the southern part of Zealand according to Deichmann-Branth and Rostrup (1869, p. 253).

ETYMOLOGY.—From the generic name of the host genus *Pertusaria*, and Latin *-icola*, dweller.

ILLUSTRATIONS.—Hawksworth *in* Trans. Br. mycol. Soc. **65**: 232, fig. 4 A-D. 1975. — ? Dibben, Chemosyst. *Pertusaria* N. Am.: 566, figs. 123—4. 1974.

EXSICCATAE.—Mougeot & Nestler, Stirpes Crypt. no. 1446 (sub *Spilomium pertusaricola*; E).

OTHER SPECIMENS EXAMINED (only ones additional to those listed in Hawksworth (1975) are cited here).—

On *Pertusaria leioplaca* (thallus): BRITISH ISLES: Sussex, Upper Beeding, Beeding Priory, on *Acer pseudoplatanus*, 20 Sept. 1973, *B. J. Coppins* (E); Oxfordshire, Bix Bottom, on *Fraxinus*, May 1975, *H. J. M. Bowen* (E). — FRANCE: *sine loc.*, Mougeot & Nestler, Stirpes Crypt. no. 1446 (E). — IRELAND: Co. Wicklow, Powerscourt Deer Park, 3 April 1976, *B. J. Coppins 1615* (E).

On *Pertusaria pertusa* (thallus): DENMARK: Zealand, Borreby, near Skelskør, on *Tilia*, *c.* 1866, *J. S. Deichmann-Branth* (C). — SPAIN: Mallorca, Umgebung von Sóller, Puerto de Sóller, an *Olea* auf den Hölzen südlich des Orles, 5 April 1964, *J. Poelt* (M).

This species is, like *L. boreale*, retained in *Lichenoconium* here only in the absence of a known alternative generic name. Many names in generic rank described in the non-lichenized and non-lichenicolous fungi have been proposed for species with spores not unlike those of *L. pertusariicola* but the application of most remains uncertain at the present time (B. C. Sutton, pers. comm.). Rather than propose a new generic name that might prove to be superfluous in a few years, it seems preferable to retain this species in *Lichenoconium* for the present. The main characters separating this species from the others treated here (excl. *L. boreale*) are (i) the very large pycnidia, (ii) the outer pycnidial wall which is ± hyaline and less rigid, (iii) the pigmented conidiogenous cells which are also almost entirely distinctly annellide-like, and (iv) the conidia which have entirely smooth walls even when viewed by SEM at ×8000 (Pl. 29E).

Lichenoconium pertusariicola appears to cause little damage to its hosts and so might perhaps be termed a parasymbiont rather than a parasite. It occupies an isolated position with respect to the remainder of the species treated here and is most unlikely to be confused with any of them.

LICHENOCONIUM PYXIDATAE (Oud.) Petr. & Syd.

Fig. 2B, Pl. 27E—H

Lichenoconium pyxidatae (Oud.) Petr. & Syd. *in* Beih. Repert. Spec. nov. Regni veg. **42**: 435. 1927. — *Coniothyrium pyxidatae* Oud. *in* Proc. K. Ned. Akad. Wet. **1900**: 242. 1900. — Holotype: Netherlands, Limburg, Valkenburg, 'in scyphis et podetiis *Cladonia pyxidatae*', 1899, *J. Rick* (L).

Pycnidia scattered, immersed below or erumpent and sometimes appearing almost superficial, subglobose to somewhat obpyriform, black, (60—)80—120(—150) µm tall and 50—80(—100) µm wide, opening by an irregular pore or split; pycnidial wall (8—)10—14(—18) µm thick, composed of 2—4 layers of pseudoparenchymatous cells; cells polyhedral, the outer thick walled and the inner with thinner walls, mainly 7—10 µm diam., the outer dark brown to almost black, the inner pale brown to hyaline. Conidiogenous cells lining the internal wall of the pycnidial cavity, phialidic or annellide-like with 1(—2) annellations, subcylindrical but becoming somewhat ampulliform towards the base, mainly hyaline and smooth-walled but occasionally becoming slightly pigmented and finely verrucose towards the apices, (5—)6—9(—11) × 1.5—2.5(—3) µm. Conidia arising singly from the apices of the conidiogenous cells, subglobose to ovoid, distinctly truncated at the base, pale brown to brown but appearing dark brown in mass, not distinctly guttulate, walls appearing almost smooth by light microscopy but shown to have a fine verruculose ornamentation by SEM (×6000), (2—)2.5—3.5(—4) × 2—3 µm.

HOSTS.—On *Cladonia arbuscula* (Wallr.) Rabenh., *C. cenotea* (Ach.) Schaer. (*fide* Galløe, 1954), *C. fimbriata* (L.) Fr., *C. incrassata* Flörke, *C. pocillum* (Ach.) O. J. Rich. and *C. pyxidata* (L.) Hoffm. This fungus generally occurs on the podetia except in *C. incrassata* where it is present on the squamules. The determination of species in the *C. chlorophaea* (Flörke ex Sommerf.) Spreng.—*C. pyxidata* complex, in which this fungus is mainly found, is often difficult even with fresh material; these problems are magnified when dealing with the old and often broken and deformed podetia on which *L. pyxidatae* is usually found and thus some of the determinations of the hosts are tentative. This species was also recorded on *C. furcata* (Huds.) Schrad. in France by Vouaux (1914) and on its subsp. *subrangiformis* (Sandst.) Pisút in Germany by Keissler (1930, sub '*L. cladoniae*'), but Vouaux's reports of it on *Evernia prunastri* (L.) Ach. (sub *Letharia arenaria* (Fr.) Harm.), *Parmelia sulcata* Tayl. (also mentioned by Bouly de Lesdain, 1910: 278) and *Physconia* aff. *venusta* (Ach.) Poelt (sub *Physcia venusta* (Ach.) Schaer.) from France are certainly erroneous; the fungus on *E. prunastri* may well have been *L. erodens* which also has small conidia.

DISTRIBUTION.—Austria, Netherlands, British Isles, Denmark, France, Germany, and Sweden.

ETYMOLOGY.—After the specific epithet of the host from which this species was first described.

ILLUSTRATIONS.—Keissler *in* Rabenh. Krypt.-Fl. **8**: 558, fig. 107a-g. 1930. — Galløe, Nat. Hist. Dan. Lich. **9**: pl. 102 figs. 673—4; pl. 104, fig. 682. 1954.

OTHER SPECIMENS EXAMINED.—AUSTRIA: Steiermark, Wölzer Tauren, Bez. Liezen, Felsen oberhalb des Plannersees, NO oberhalb der Planneralm (SO Donnersbach), 1850—1900 m, [on *Cladonia arbuscula*,] 16 July 1972, *J. Poelt* (hb. Poelt 12340); Steiermark, Tauplitz Alm, zwischen Wurzeln und Steinen, Südseite des Traweng, oberhalb der Grazer Akademiker Hütte, [on *Cladonia* aff. *pocillum*,] 2 July 1972, *P. Döbbeler* (hb. Poelt 11569). — BRITISH ISLES: England, East Suffolk, Dunwich, on old podetia of *Cladonia* sp., on fixed shingle, 29 May 1966, *S. A. Manning* (IMI 142509). — FRANCE: La Malgrange, mur du potager sicquant, sur partie siche de *Cladonia pyxidata*, 14 Feb. 1907, *l'Abbé Vouaux* (hb. Vouaux). —

SWEDEN: Västergötland, Mt. Hunneberg, Flo parish, Laggemossen, vertical walls of peat on a drained bog, on *Cladonia incrassata*, 24 Sept. 1961, *R. Santesson 14402b* (UPS).

Keissler (1930) attempted to distinguish between two *Lichenoconium* species on *Cladonia* separated by the reaction of the host which he considered became blackened in one (named *L. cladoniae*) and remained its normal colour in the other (named *L. pyxidatae*). This is clearly not a satisfactory criterion for species delimitation, particularly as different hosts were involved, and so Clauzade & Roux (1976) rightly united them; the name *L. cladoniae*, however, is based on a species of *Abrothallus* de Not. and *L. usneae* and so cannot be taken up for this species (see p. 192). While *L. pyxidatae* appears to be confined to species of *Cladonia*, it should be noted that *L. usneae* can infect at least *C. arbuscula* and *C. cariosa*.

Infected podetia are generally darker in colour than is usual and when old and dying tend to become blackened around the pycnidia. The fungus appears to be parasitic but restricted to vegetative tissues and has not been noted in the apothecia of any infected *Cladonia* by me. In the case of infection in *C. incrassata*, large decolourised almost bleached lesions are formed in the colonies of compacted squamules; the most infected squamules becoming particularly densely sorediate. In this instance the pycnidia are rather sparse in some parts of the lesions so one might question whether *L. pyxidatae* was the primary pathogen or an opportunist in this case.

Lichenoconium pyxidatae resembles *L. erodens*, with which it has been confused in the past, in the small size of the conidia but differs in several important respects apart from occurring on different hosts, viz. the very much larger and generally mainly superficial pycnidia, the longer and narrower conidiogenous cells, and the smoother-walled and somewhat paler brown conidia which are distinctly truncated and not ± globose.

Lichenoconium usneae (Anzi) D. Hawksw., *comb. nov.*

Fig. 2C, Pl. 28A—K

Epicoccum usneae Anzi *in* Atti Soc. ital. Sci. nat. **11**(4): 181 [p. 25 of reprint]. 1868 (basionym). — Isotype: Italy, 'in disco apotheciorum *Usneae barbatæ* [*U. filipendula* aggr.] in silvis Bormiensibus opacioribus (Cerdécco)', *Anzi*, Lich. rar. Langob. exs., fasc. 13, no. 523 (K; two packets). — *Coniothyrium usneae* (Anzi) Vouaux *in* Bull. trimest. Soc. mycol. Fr. **30**: 295. 1914.

Coniothyrium imbricariae Allesch. *in* Ber. bayer. bot. Ges. **5**: 18. 1897. — Holotype: Germany, 'in disco nigrifacto apotheciorum *Imbricariæ aspidotae* [*Parmelia exasperata*] Oberammergau, Aug. 1896', *Schnabl* (M). — *Lichenoconium imbricariae* (Allesch.) Keissl. *in* Rabenh. Krypt.-Fl. **8**: 565. 1930.

Coniothyrium jaapii Died. *in* Kryptfl. Mark Brandenb. **9**: 573. 1914. — Lectotype: Germany, 'auf den Apothezien von *Parmelia conspersa*, Triglitz l.d. Prignitz', 8 April 1898, *O. Jaap* (HBG). — *Lichenoconium jaapii* (Died.) Petr. & Syd. *in* Beih. Repert. Spec. nov. Regni veg. **42**: 435. 1927.

Coniothyrium lecanoracearum Vouaux *in* Bull. trimest. Soc. mycol. Fr. **30**: 293. 1914; nom. illegit. (Art. 70). — Isosyntype: Canada, British Columbia, Vancouver Island, Victoria, on *Lecanora pacifica* on trunks of poplars, 22 May 1893, *J. Macoun*, Merrill, Lich. Exs. no. 8 (UPS). — *Lichenoconium lecanoracearum* (Vouaux) Petr. & Syd. *in* Beih. Repert. Spec. nov. Regni veg. **42**: 434. 1927.

Pycnidia scattered to loosely aggregated, mainly immersed or mainly erumpent to almost superficial, subglobose to almost cupuliform, black, (40—)50—80(—110) µm diam., opening by an irregular and often conspicuous pore; pycnidial wall mainly 6—10 µm thick, composed of (1—)2—3 layers of pseudoparenchymatous cells; cells polyhedral to rounded, rather thick-walled, mainly (3—)4—7(—9) µm diam., the outer dark brown or brown, the inner pale brown to hyaline. Conidiogenous cells lining the internal wall of the pycnidial cavity, phialidic or annellide-like with 1 annellation, subcylindrical to ampulliform, hyaline and smooth-walled throughout or becoming pigmented and verrucose apically to varying degrees, (5—)7—9(—11) × (2—)2.5—3.5(—4) µm. Conidia arising singly from the apices of the conidiogenous cells, globose to subglobose, sometimes appearing rather angular but usually not distinctly truncated at the base, brown singly but appearing almost black in mass, not distinctly guttulate; walls usually appearing distinctly verrucose or more exceptionally almost smooth by light microscopy but seen to have a verruculose ornamentation by SEM (×6000), (2.5—) 3—4 (—5) µm diam.; abnormally developed ellipsoid conidia to about 7×3.5 µm occur very rarely in some pycnidia.

HOSTS.— On thalli and (or) apothecia of numerous lichens including *Alectoria fuscescens* Gyeln., *Anaptychia ciliaris* (L.) Körb., *Cladonia arbuscula* (Wallr.) Rabenh., *C. cariosa* (Ach.) Spreng., *Hypogymnia physodes* (L.) Nyl., *Lecanora pacifica* Tuck., *Parmelia conspersa* (Ehrh. ex Ach.) Ach., *P. exasperata* (Ach.) de Not. (syn. *P. aspera* Massal., *P. aspidota* (Ach.) Poetsch), *P. glabratula* (Lamy) Nyl. subsp. *glabratula* and subsp. *fuliginosa* (Fr. ex Duby) Laund., *P. olivacea* (L.) Ach., *P. pulla* Ach. (syn. *P. prolixa* (Ach.) Carroll), *P. rudecta* Ach., *P. saxatilis* (L.) Ach., *P. verruculifera* Nyl. (syn. *P. isidiotyla* auct.), *Physica aipolia* (Ehrh. ex Humb.) Hampe, *P. stellaris* (L.) Nyl. em. Harm., *Physconia pulverulenta* (Schreb.) Poelt, *Ramalina* aff. *baltica* Lett., *R. calicaris* (L.) Fr., *R. siliquosa* (Huds.) A.L.Sm., *R. subgeniculata* Nyl. and *Usnea filipendula* Stirt. aggr. (syn. *U. barbata* auct.). Also reported by Vouaux (1914, sub *C. imbricariae*) on *Evernia prunastri* (L.) Ach. and *Parmelia sulcata* Tayl. but these records may be errors for another species (e.g. *L. parasiticum*). There is also a reference to its occurrence on *Cornicularia aculeata* (Schreb.) Ach. by Bachmann (1926, sub *Coniothyrium imbricariae*) when the pycnidia were about 70×60 µm and the conidia '3.1—3.2×2.8' µm, but that record requires confirmation.

DISTRIBUTION.—Austria, British Isles, Canada (B.C.), Canary Islands, Czechoslovakia, Denmark, Germany, Ireland, Italy, Norway, Spain, Sweden, Switzerland, and the U.S.A. (Missouri, New Jersey). Several specimens on a range of hosts were reported from France by Vouaux (1914, sub *C. imbricariae*) but no collections from that country have been seen by me.

ETYMOLOGY.—After the host genus from which this species was first described.

ILLUSTRATIONS.—Hawksworth *in* Trans. Br. mycol. Soc. **67**: 54, fig. 2A-D; 55, fig. 3D. 1976. — ? Bachmann *in* Hedwigia **66**: 334, fig. 9. 1926.

EXSICCATAE.—Anzi, Lich. rar. Langob. exs., fasc. 13, no. 523 (sub *Epicoccum usneae*; K). — Arnold, Lich. Exs. no. 1718 (sub *Epicoccum usneae*; K). — Ellis & Everh., N. Am. Fungi Exs., ser. 2, no. 2383 p.p. (sub *Sphaeropsis cladoniae*; K, M). — Hepp, Flecht. Eur. no. 775 (sub *Imbricaria dendritica* b. *maritima*; E). — Leighton, Lich. Br. Exs. nos. 263 (sub *Parmelia olivacea*; E), 356 (sub *P. olivacea* var. *exasperata*; E). — Merrill, Lich. Exs. no. 8 (sub *Lecanora pacifica*; UPS). — Mudd, Lich. Br. Exs. no. 72 (sub *Parmelia olivacea*; E). — Rabenh., Wint. & Pazsch., Fungi Eur. no. 3891 (sub *Sphaeropsis cladoniae*; K).

OTHER SPECIMENS EXAMINED.—On *Alectoria fuscescens* (thallus): BRITISH ISLES: Scotland, Perthshire, Glen Lyon, old wood of Meggernie, on *Betula*, 25 July 1974, *B. J. Coppins 1781b* (E; with *Phacopsis huuskonenii*).

On *Anaptychia ciliaris* (thallus): SPAIN: prov. Alava, near Murua (c. 15 km n.n.w. of Vitoria), alt. 600 m, on *Quercus robur*, 8 May 1959, *R. Santesson 13285e* (UPS; see also Santesson, 1960). — Sweden: Uppland, Lagga s:n, Norredatorp, på asp, 10 Aug. 1952, *R. Santesson* (UPS).

On *Cladonia arbuscula* (podetia): British Isles: Scotland, Fifeshire, Tentsmuir Reserve, 10 June 1976, *B. J. Coppins 1884* (E; IMI 205335).

On *Cladonia cariosa* (apothecia): U.S.A.: Missouri, near Emma, April 1889, *C. H. Demetrio*, Ellis & Everh. N. Am. Fungi Exs., ser. 2, no. 2383 p.p. (K, M); *loc. cit.*, Oct. 1890, *C. H. Demetrio*, Rabenh., Winter & Pazsch. Fungi Eur. no. 3891 p.p. (K) [both exsiccatae with *Abrothallus* sp.: see p. 192].

On *Hypogymnia physodes* (thallus): Sweden: Härjedalen, Tännäs parish, Mt. Ramundberget, eastern slope, *c.* 1 km s. of Hotel Ramundberget, alt. 800—900 m, on *Betula pubescens*, 4 Sept. 1970, *R. Santesson 22663b* (UPS).

On *Parmelia conspersa* (apothecia; rarely also thallus): British Isles: Scotland, Dumfrieshire, Moffat, near Broomlands, 15 Aug. 1856, [collector unknown] (E); Wales, Cardiganshire, Strata Florida, on stone wall by farm, 4 April 1968, *B. J. Coppins* (E). — Germany: Nohnsen (Holsheim), auf Steinen, 22 June 1902, *O. Jaap* (HBG). — Sweden: Östergötland, Väversunda s:n, Marsasläpan, on boulder in a copse, 2 July 1948, *R. Santesson* (UPS); Skåne, Rörum s:n, between Nygård and Mossaryd, on boulder in a copse, 9 July 1947, *R. Santesson* (UPS).

On *Parmelia exasperata* (apothecia): British Isles: England, Herefordshire, Pembridge, *W. A. Leighton*, Lich. Exs. no. 356 (E); Yorkshire, Cleveland, on *Fraxinus*, Sept. 1859, *A. C. Maingay* (E), Cleveland, near Ayton, trees, *W. Mudd*, Lich. Br. Exs. no. 72 and Leight., Lich. Br. Exs. no. 263 (E); Scotland, Kirkcudsbrightshire, New Galloway, Kenmure Holms, July 1890, *J. M'Andrew* (E); East Inverness, Fort Augustus, 23 Aug. 1856, *W. L. Lindsay* (E). — Norway: Sör-Tröndelag, Rissa parish, in the valley of the river Sörelv, on *Alnus incana*, 31 July 1961, *R. Santesson 14316c* (UPS). — Sweden: Jämtland, Brunflo s:n, Brunflo kyrkogård, on *Sorbus*, 18 Aug. 1948, *R. Santesson 48.509* (UPS).

On *Parmelia glabratula* subsp. *glabratula* (thallus): Austria: Grazer Bergland, Steiermark, Teichalpe, Breitalmhalt, alt. 1350 m, auf *Acer pseudoplatanus*, 9 Aug. 1973, *J. Poelt* (hb. Poelt 12287). — On subsp. *fuliginosa* (thallus): British Isles: England, Yorkshire, near Clapham, Oct. 1857, *Carrington* (E). — Switzerland: Wallis, Aletschwald ob Brig, beschattete Überhangfläche, alt. 2000 m, 11 Sept. 1968, *J. Poelt* (hb. Poelt 6359).

On *Parmelia olivacea* (apothecia; rarely also thallus): Norway: Oppland, Vågå parish, s.w. slope of Mt. Vole, alt. 700 m, on birch, 25 July 1961, *R. Santesson 14169c* (UPS). — Sweden: Jämtland, Undersåker s:n, Stornlvåstugan, on birch, 3 Aug. 1950, *R. Santesson* (UPS), Åre s:n, Handölsfallen, on birch, alt. 650 m, 4 Aug. 1948, *R. Santesson 48.245c* (UPS), Åre s:n, Brännholmen i Ånnsjön, on birch, 25 Feb. 1952, *R. Santesson* (UPS), Åre s:n, Storlien, *c* 1 km n.w. of the railway station, alt. 650 m, on birch, 23 Feb. 1957, *R. Santesson 11702* (UPS), Åre s:n, n.e. slope of Snasahögarna, on birch, alt. 800 m, 16 Aug. 1948, *R. Santesson 48.624* (UPS); Torne Lappmark, Jukkasjärvi s:n, Abisko Nationalpark, alt. 450 m, 9 Aug. 1944, *R. Santesson* (UPS), Jukkasjärvi s:n, Lake Torneträsk District, Abisko, west of the Natural Science Research Station, alt. 350 m, on *Betula tortuosa*, 23 June 1952, *C. G. Alm* (UPS; with *L. xanthoriae*), Jukkasjärvi s:n, e. slope of Slåttatjåkko, alt. 500 m, 10 Aug. 1947, *R. Santesson* (UPS); Västergotland, Töreboda, Gastorp, 26 June 1961, *J. Lundberg* (UPS).

On *Parmelia pulla* (apothecia): Ireland, Co. Dublin, au Felsen, *D. Moore*, Hepp, Flecht. Eur. no. 775 (E; isotype of *Imbricaria dendritica* b. *maritima* Hepp). — Sweden: Skåne, Rörum s:n, between Nygård and Mossaryd, on boulder in a copse, 9 July 1947, *R. Santesson* (UPS).

On *Parmelia rudecta* (thallus); U.S.A.: New Jersey, near Atsion, Burlington Co., 1 Sept. 1957, *M. E. Hale 15258* (UPS).

On *Parmelia saxatilis* (apothecia): CZECHOSLOVAKIA: Carpati, montes Liptovské hole, in monte 'Suchy hrádok, alt. 1500 m, ad cortices *Picearum*, Aug. 1963, *A. Vezda* (hb. Vezda).

On *Parmelia verruculifera* (apothecia): SWEDEN: Skåne, Brunnby s:n, s. of Kullagård, 18 July 1947, *R. Santesson* (UPS).

On *Physcia aipolia* (apothecia; rarely also thallus): BRITISH ISLES: Scotland, East Inverness, Drumnadrochit, between Divach Lodge and Farm, alt. 500 ft, on *Acer pseudoplatanus*, 22 June 1975, *B. J. Coppins 1387a* (E). — SWEDEN: Jämtland, Brunflo s:n, Torvalla, on aspen, 18 Aug. 1948, *R. Santesson 48.501* (UPS): Östergötland, Rogslösa s:n, Borghamn, near the railway station, 11 July 1948, *R. Santesson 48.174* (UPS).

On *Physcia stellaris* (apothecia): SWEDEN: Gotland, Öja s:n, Burgsvik, on *Prunus cerasus*, 16 July 1952, *R. Santesson* (UPS); Västergötland, Gärdhems s:n, *c.* 1 km n.n.w. of Lundens gård, on aspen, 27 March 1948, *R. Santesson* (UPS).

On *Physconia pulverulenta* (thallus): DENMARK: Lolland, Radsted, on *Ulmus* in an avenue near the manor house Krenkerup, alt. 0—10 m, 20 May 1976, *M. Skytte Christiansen 76.071* (hb. Christiansen 116).

On *Ramalina* aff. *baltica* (thallus): SWEDEN: Uppland, Alsike s:n, Kungseken, 30 March 1948, *G. E. DuRietz* (UPS).

On *Ramalina calicaris* (apothecia and thallus): BRITISH ISLES: England, South Devon, Slapton, Duck Marsh, on *Salix*, *D. L. Hawksworth 3770* (IMI 186833; see also Hawksworth, 1976).

On *Ramalina siliquosa* (thallus): BRITISH ISLES: Shetland Islands, Ronas Hill, on granite, Aug. 1966, *D. L. Hawksworth 218c* (IMI 191488; poor material, see also Hawksworth, 1976).

On *Ramalina subgeniculata* (apothecia and thallus): CANARY ISLANDS: Tenerife, Aguamansa, on twigs of *Pinus* along the road to Teide, alt. 1200 m, 25 Dec. 1975, *M. Skytte Christiansen 75. 537b* (hb. Christiansen 94).

On *Usnea filipendula* aggr. (apothecia): ITALY: Tirol, Zweigen im Walde gegen Roen auf der Mendel oberhalb Bozen, 13 Aug. 1896, *F. G. C. Arnold*, Lich. Exs. no. 1718 (K).

In common with *Lichenoconium parasiticum*, *L. usneae* has a rather wide host range but, unlike that species, it shows a strong preference for the apothecia of species of *Parmelia*, the Physciaceae and the Ramalinaceae. Infected apothecial discs may become blackened, as with infections by *L. parasiticum*, or decolourised or, more rarely, almost bleached. In *Parmelia* and *Physcia* species where the fungus is normally restricted to the apothecia, pycnidia occur occasionally in the thalline margin or on the underside of the discs, but spread onto adjacent parts of the thalli only exceptionally; where thalli become colonised in this manner they almost invariably appear to be already damaged in some way, as by snail grazing (e.g. *Parmelia conspersa*, *Santesson*, 1947, UPS) or by other lichenicolous fungi (e.g. *Abrothallus parmeliarum* on *P. olivacea*, *Alm*, 1952, UPS; *Phoma physciicola* on *Physcia aipolia*, *Coppins 1387a*, E). When thalli alone are known to be colonised these are also often discoloured, most frequently to shades of brown, but again the infected thalli often appear to be already in a damaged state though the reasons for this are not always clear; other lichenicolous fungi may be associated in at least some cases (e.g. *Cornutispora lichenicola* on *Parmelia glabratula* subsp. *fuliginosa*, hb. Poelt 6359). In other instances infected thalli of the same host may be almost normal in colour or extensively discoloured (e.g. *Anaptychia ciliaris*). In the infected *Alectoria fuscescens* specimens seen, the pycnidia are localised in blackened geniculately deformed areas on branches where the symptoms are characteristic of *Phacopsis huuskonenii* Räs. with which it is mixed. The black-bordered reaction spots in foliose thalli so characteristic of infections by *L. erodens* and *L. parasiticum* in particular, never seem to be developed by the host in response to infections by *L. usneae*; the different symptoms when *Hypogymnia physodes* is colonised by *L. erodens* and *L. usneae* is particularly striking, no black border or necrotic spot being developed (compare Pl. 23A—C with Pl. 28A—B). These observations suggest that *L. usneae* is generally not an important pathogenic species but rather a parasymbiont with opportunistic tendencies.

Infected apothecia in *Usnea filipendula* aggr., and also to some extent in *Lecanora pacifica*, assume a characteristic bluish-grey hue but this is perhaps merely a host response as similarly tinted apothecia occur in *Ramalina calicaris* infected with *Abrothallus suecicus* Nordin (Hawksworth, 1976); in the latter host *L. usneae* tends to produce a brownish or blackish discolouration and also to occur on the thallus as well. In one isotype of *L. usneae* seen pycnidia occur under the discs as well as in the hymenium.

Keissler (1930) retained *Epicoccum usneae* in *Coniothyrium* and did not transfer it to *Lichenoconium* on account of the presence of a distinct ostiole rather than an irregular pore; in fact Anzi's material does not have a cellularly differentiated ostiole but an

TABLE V

LICHENOCONIUM USNEAE: VARIATION IN SELECTED CHARACTERS ON DIFFERENT HOSTS

Host	Pycnidia (μm)	Phialides (μm)	Conidia (μm)
Alectoria fuscescens	60—80	(6—)7—9×3—3.5	(2.5—)3—4(—5)
Cladonia arbuscula	50—75	7—8×3	3—4(—5)
Hypogymnia physodes	(50—)70—80	7—10×2—3(—3.5)	3—4(—4.5)
Lecanora pacifica	50—75	6—9×3—3.5	3—4(—4.5)
Parmelia conspersa	(40—)50—80	7—8×2—3	2.5—3.5(—4)
P. exasperata	(30—)50—80(—85)	6—9×2.5—3.5	(2.5—)3—4(—5)
P. glabratula	50—70	8—10×2—3	3—4(—5)
P. olivacea	50—80(—100)	6—8×3—3.5	(2.5—)3—4(—4.5)
P. pulla	50—75	6—8×2—3.5	3—4(—5)
P. rudecta	(40—)50—75	6—9×2.5—3	(2.5—)3—3.5(—4)
P. saxatilis	60—80	few seen	(3—)3.5—4
P. verruculifera	60—90(—100)	7—9×3—4	(3—)3.5—4(—4.5)
Physcia aipolia	(50—)60—80(—90)	8×3	(2.5—)3—4(—4.5)
P. stellaris	75—80	6—8(—11)×3—3.5	3—4(—4.5)
Physconia pulverulenta	60—80	7—10×3—3.5	3—4(—4.5)
Ramalina aff. *baltica*	45—55	6—8×3—3.5	3—4
R. calicaris	50—60	6—8×3—4	3.5—5
R. subgeniculata	50—80	(5—)6—7×3	3—4(—5)
Usnea filipendula aggr.	60—90(—110)	7—10×2.5—3.5	3—4

irregular opening to 75 µm wide and agrees in its anatomical details with the species termed *L. imbricariae* by him; they are thus regarded as synonyms here. Keissler also indicated that this fungus was available in Jaap's, Fungi Sel. Exs. no. 74 but the material of this number in K only had pycnidia of *Abrothallus parmeliarum*. The host of the isotype of *Epicoccum usneae* belongs in the taxonomically poorly known *Usnea filipendula* group and was found to contain salazinic and usnic acids and a trace of an unknown compound by thin-layer chromatography.

Lichenoconium usneae is a rather constant species in most respects and such variations as do occur on different hosts (see Table V) are scarcely taxonomically important. The degree to which the apices of the conidiogenous cells become pigmented is extremely variable but as hyaline and pigmented ones can occur in a single pycnidium this appears to be of little significance. *L. usneae* differs from *L. parasiticum* in the longer conidiogenous cells and from *L. xanthoriae* in the smaller pycnidia; the joint occurrence of *L. usneae* and *L. xanthoriae* in the apothecia of a single specimen of *Parmelia olivacea* (*Alm*, 1952; UPS) when they remain quite distinct supports their recognition in species rank.

In the absence of any extant material in B (B. Hein, *in litt.*) an isotype of *Coniothyrium jaapii* from Jaap's herbarium now in HBG is designated as lectotype for that name here. The typification of *Coniothyrium lecanoracearum* presented some difficulties as although Vouaux (1914) mentioned some nine specimens (syntypes) from different host species none are now present amongst his remaining collections (Rondon, 1969; and *in litt.*). There can be little doubt that Vouaux's concept of this species included both *L. parasiticum* (from the hosts indicated) and *L. usneae* (from the conidiogenous cell size given) as understood here and probably also *Muellerella hospitans* Stiz. (an ascomycete in the apothecia *Bacidia rubella*). An isosyntype on *Lecanora pacifica* in UPS was located but proved to be *L. usneae* and not *L. lecanoracearum* as understood by Petrak & Sydow (1927) having conidiogenous cells (6—)7—9×3—3.5 µm. Vouaux's name is thus best rejected as based on discordant elements (Art. 70).

LICHENOCONIUM XANTHORIAE M.S. Christ.

Fig. 2D, Pl. 29D, F—J

Lichenoconium xanthoriae M.S. Christ., Friesia **5**: 212. 1956. — Holotype: Denmark, Jutlandia borealis, par. Råbjærg, in apotheciis *Xanthoriae polycarpae*, 26 June 1942, *M. Skytte Christiansen* (C).

Pycnidia scattered to somewhat aggregated, immersed below but becoming erumpent above when mature, subglobose to almost cupuliform, black, (80—)100—175 (—200) µm diam., opening by an irregular pore; pycnidial wall 6—12(—15) µm thick, composed of 2—4 layers of pseudoparenchymatous cells; cells polyhedral to rounded, rather thick-walled, mainly 5—10×3—7 µm, the outer dark brown or brown, the inner pale brown to hyaline. Conidiogenous cells lining the internal wall of the pycnidial cavity, phialidic or annellide-like with 1 annellation, subcylindrical to somewhat ampulliform, usually hyaline and smooth-walled but sometimes becoming slightly pigmented and verrucose apically, (5—)6—8(—11) × (2—)2.5—4 µm. Conidia arising singly from the apices of the conidiogenous cells, globose to subglobose, truncated at the base, sometimes appearing slightly angular, brown singly but appearing almost black in mass, not distinctly guttulate; walls appearing slightly verrucose to almost smooth by light microscopy but seen to have a coarse verrucose ornamentation by SEM (×6000), (2.5—)3—4.5(—6) µm diam.

HOSTS.—On *Cetraria sepincola* (Ehrh.) Ach. (apothecia), *Xanthoria parietina* (L.) Th. Fr. (apothecia and thallus), *X. polycarpa* (Hoffm.) Oliv. (apothecia; particularly common on this host) and possibly also *Parmelia olivacea* (L.) Ach. (apothecia; see below).

DISTRIBUTION.—British Isles, Czechoslovakia, Denmark and Sweden.

ETYMOLOGY.—After the host genus from which this species was first described.

ILLUSTRATIONS.—Christiansen *in* Friesia **5**: 213 fig. 1, 214 fig. 2a-e. 1956.

OTHER SPECIMENS EXAMINED.—On *Cetraria sepincola*: BRITISH ISLES: Wales, Radnorshire, Llyn Mire, Aug. 1972, *P. J. Beckett* (IMI 189905). — SWEDEN: Västergötland, Mårdaklev, on *Alnus glutinosa*, 27 March 1975, *M. Skytte Christiansen 75.010* (hb. Christiansen).

On *Parmelia olivacea*: SWEDEN: Torne Lappmark, Jukkasjärvi parish, Lake Torneträsk District, Abisko, west of the Research Station, alt. c. 350 m, on *Betula tortuosa*, 23 June 1952, *C. G. Alm* (UPS; with *L. usneae*).

On *Xanthoria parietina*: BRITISH ISLES: Scotland, Banffshire, Glen Avon, Inchrory Lodge, alt. 1300 ft, 10 July 1975, *B. J. Coppins 901* (E). — CZECHOSLOVAKIA: Moravia, Rouchovany, in valle fluvii Rouchovanka prope Nové dvory, *c.* 360 m, ad *Populus*, Aug. 1971, *A. Vezda* (hb. Rondon, hb. Vezda); Moravia, prope pagum Hvozd procul opp. Litovel, alt. 500 m, 3 Sept. 1962, *A. Vezda*, Fungi Lichenicoli Exs,. s.n. (K, hb. Rondon).

On *Xanthoria polycarpa*: BRITISH ISLES: England, North Somerset, Glastonbury, Shapwick Heath, on *Salix*, 27 March 1967, *P. W. James* (BM); England, South Northumberland, Comb, 27 March 1976, *M. R. D. Seaward* (IMI 203614); Scotland, Angus, near Auchmithie by Arbroath, on *Crataegus*, Feb. 1967, *U. K. Duncan* (E); Scotland, Fife, St. Andrews, Kittock's Den, 17 Feb. 1974, *P. Harrold* (E). — DENMARK: Anholt, Ørkenen, on *Juniperus communis*, 9 July 1941, *M. Skytte Christiansen 6185* (hb. Christiansen); E Jutland, Agri parish, Mols Bjærge, Strandkær, on *Crataegus*, 11 April 1943, *M. Skytte Christiansen 10404* (hb. Christiansen); South Jutland, Skærbæk parish. on *Salix aurita*, 17 Aug. 1944, *M. Skytte Christiansen 12352* (hb. Christiansen); West Jutland, Oksby parish, Krogsande, on *Sarothamnus scoparius*, 4 Aug. 1941, *M. Skytte Christiansen 7268* (hb. Christiansen), on pear tree, 4 Aug. 1941, *M. Skytte Christiansen 7271* (hb. Christiansen); West Jutland, Ho parish, on *Sarothamnus scoparius*, 5 Aug. 1941, *M. Skytte Christiansen 7409* (hb. Christiansen), on heather in the roof of an old shed, 23 July 1941, *M. Skytte Christiansen 6937a* (hb. Christiansen); Lolland, Thoreby parish, Sundby, on *Sambucus*, 29 May 1943, *M. Skytte Christiansen 10635* (hb. Christiansen); Zealand, Solrød parish, on *Populus tremula*, 29 Sept. 1940, *M. Skytte Christiansen 5908* (hb. Christiansen); Zealand, Kildebrønde parish, Hundige, on *Aesculus hippocastanum*, 30 March 1938, *M. S. Christiansen 2403* (hb. Christiansen); Zealand, Årby parish, Asnæs, on *Prunus spinosus*, 10 Aug. 1944, *M. Skytte Christiansen 12256a* (hb. Christiansen); Zealand, Holbaek, Tveje Merløse, on a fencing post, 26 Aug. 1941, *M. Skytte Christiansen 7621* (hb. Christiansen). — SWEDEN: Östergötland, Rogslösa s:n, Borghamn, north-east of village, on *Salix*, 24 June 1948, *R. Santesson 4888* (hb. Christiansen); Västergötland, Trollhattan, Staveredslund, Lillgården, on *Acer*, 23 June 1948, *R. Santesson 4883* (hb. Christiansen, M).

This fungus has been ably discussed by Christiansen (1956) who provides detailed information on the symptoms developed in *Xanthoria polycarpa*. He noted that the thecium (hymenium) of infected apothecia was somewhat damaged containing few asci with ascospores and no young asci or deeply staining ascogenous hyphae. The apothecial discs of the host are at first not discoloured but with age the abundance of pycnidia, and conidia which become scattered over the surface, together make the apothecia appear as if blackened by soot. In the case of infected apothecia of *Cetraria sepincola*, *Parmelia olivacea* and *Xanthoria parietina* similar symptoms develop but in the latter pycnidia may also form on the thallus, which they damage, so large areas of the thallus also assume a blackened appearance. Specimens of *Xanthoria parietina* infected by the dematiaceous hyphomycete *Xanthoriicola physciae* (Kalchbr.) D. Hawks. (see Hawksworth & Punithalingam, 1973) resemble those affected by *L. xanthoriae* superficially, although closer examination will show the absence of pycnidia and sections the presence of branched conidiophores in the case of *X. physciae*.

Christiansen (1956) noted that this fungus resembled *L. lichenicola* in its large pycnidia, but differs from that species in the size and shape of the conidia. *L. cargillianum*, which also has large pycnidia, differs from *L. xanthoriae* in the larger conidia.

In the collection on *Parmelia olivacea* referred to this species here, the conidia are somewhat larger than is usual for *L. xanthoriae* and measure (4—)5—6(—6.5) μm diam. The conidia in this collection differ from those of *L. lichenicola* in shape; also, that species has longer conidiogenous cells. As the conidia are also smaller and much less coarsely verrucose than in *L. cargillianum*, this specimen is referred to *L. xanthoriae* here, albeit with some hesitation. Although numerous specimens of *P. olivacea* infected by *Lichenoconium usneae* have been found, only in this one has a member of this genus with large (to 200 μm diam.) pycnidia and spores in this size range been discovered (this specimen is also infected by *L. usneae* although that species tends to occur in different apothecia on it).

EXCLUDED TAXA

cladoniae. — *Lichenoconium cladoniae* (Ellis & Everh.) Petr. & Syd. *in* Beih. Repert. Spec. nov. Regni veg. **42**: 433. 1927. — *Sphaeropsis cladoniae* Ellis & Everh. *in* J. Mycol. **5**: 149. 1889. — *Coniothyrium cladoniae* (Ellis & Everh.) Sacc., Syll. Fung. **10**: 268. 1892.

This fungus was first reported from the apothecia of *Cladonia cariosa* (Ach.) Spreng. in the U.S.A. (Missouri, near Emma, April 1889, *C.H. Demetrio*) and isotypes were sent out in Ellis & Everhart's N. Am. Fungi. Exs., ser. 2, no. 2383 (K, two sets; M) and topotypes collected in 1890 distributed in Rabenhorst, Winter & Pazschke's Fungi Eur. Exs. no. 3891 (K, two sets). The material comprises two lichenicolous fungi, an *Abrothallus* in which the ascospores become separated at maturity (R. Santesson, *in litt.*), and a *Lichenoconium* agreeing with *L. usneae* as treated above. The original description certainly included the *Lichenoconium* element but the *Abrothallus* is perhaps principally responsible for the dark discolouration of the fruits and the *Lichenoconium* may well be opportunist as it is on many other hosts. This case has been investigated in detail by Santesson (*in litt.*) who considers the epithet to be correctly used in *Abrothallus*; as this name will be fully discussed by him in a future publication it is not treated further here.

Most literature references to this species refer to *L. pyxidatae* which has smaller and smoother conidia and larger pycnidia than the *Lichenoconium* on *C. cariosa*. Keissler (1930) used the epithet for material like *L. pyxidatae* that discoloured infected podetia. The reference of Sutton (1973) to *L. cladoniae* is based on material in IMI now referred to *L. pyxidatae*.

cyanescens. — *Oospora cyanescens* (Hazsl.) Sacc. & Vogl *in* Saccardo, Syll. Fung. **4**: 25. 1886. — *Torula cyanescens* Hazsl. *in* Kalchbrenner, Mat. természettud. Közl. **3**: 296. 1855 [not seen] and *in* Hedwigia **4**: 120. 1856.

This taxon was originally reported to produce almost hyaline conidia in short moniliform chains comprising 3—10 conidia. Vouaux (1913) accepted it in *Oospora* but Keissler (1930), basing his opinion on the information provided by Hazslinsky, considered that this species should be treated as a synonym of *Coniothyrium usneae* (see p. 185). *Torula cyanescens* was described on the basis of material collected on '*Usnea barbata*' in Hungary by Kalchbrenner but unfortunately no material under these names appears to be extant amongst the Hazslinsky and Kalchbrenner herbaria now in BP (Dr J. Gönczöl, *in litt.*). As no information as to conidial size was provided, as there is no evidence that the spores were brown, and as it is unknown if they even arose from pycnidia, in the absence of type material it appears most unwise to follow Keissler (1930) and treat this taxon as identical with *C. usneae*.

epiphyllum. — *Coniothyrium epiphyllum* Vouaux *in* Bull. trimest. Soc. mycol. Fr. **30**:296. 1914.

This name was introduced by Vouaux on the basis of a brief report of a pycnidial fungus with 'jaune-pale' conidia 4.2 × 3.2 µm by Lindsay (1859: 277). An examination of the material preserved in E, presumably that studied by Lindsay and thus the holotype for Vouaux's name (British Isles, England, Leicestershire, Gopsall, on laurel [cf. *Prunus laurocerasi*] &c. leaves, [*A. Bloxam*]; Leighton, Lich. Br. Exs. no. 103) showed it to support two non-lichenized fungi: (a) *Seuratia millardetii* (Racib.) Meeker (syn. *Atichia glomerulosa* (Ach. ex Mann) Stein, *Collema epiphyllum* Leight.), and (b) *Chaetothyrium babingtonii* (Berk.) Keissl. The *Chaetothyrium* predominates on the collection and is fertile but no pycnidia were detected on it. Lindsay clearly indicated that his pycnidia were associated not with the *Seuratia* (as stated by Vouaux, 1914) but with the *Chaetothyrium*, however, and that they were '... quite superficial, removeable by the slightest touch; ...'. It seems probable that all have become rubbed off during the subsequent 117 years and thus the identity of this fungus remains uncertain at the present time.

harmandii. — *Coniothyrium harmandii* Zopf ex Vouaux *in* Bull. trimest. Soc.

mycol. Fr. **30**: 295. 1914. — *Coniothyrium* sp. Zopf *apud* Harmand *in* Bull. Soc. bot. Fr. **53**: 74. 1906; nom. inval. (Arts. 32, 34, etc.)

This taxon, reported from material of *Pertusaria melaleuca* (Turn. & Borr.) Duby (now generally regarded as a synonym of *P. pustulata* (Ach.) Duby) collected by V. A. Cordiero in Portugal was first recognised as distinct by Zopf (Harmand, 1906) who did not give it a name. Vouaux (1914), in view of his extensive description, must have seen Cordiero's material, and he indicated that the conidiophores (or conidogenous cells) were generally once- or twice-branched (only rarely simple) and the conidia 2.5—4 × 2—2.5 µm. No material of this fungus is now present in the herbaria of Vouaux (*fide* Rondon, 1969, and *in litt.*), Zopf (B, *fide* B. Hein, *in litt.*) or Harmand (ANGUC, *fide* M. Guerlesquin, *in litt.*; DUKE, *fide* M. Watkins *in litt.*) and the location of any separate herbarium Cordiero may have formed is unknown (Grummann, 1974: 769). In ANGUC there is, however, a specimen labelled '*Pertusaria melaleuca* Dub. environs d. Letutuias (Cortugao) leg. *Cordiero* 1904 no. 746' but there is no annotation to indicate that the lichenicolous fungus was on this and none could be found on it; nevertheless, this is almost certainly the collection in which Harmand found the fungus but he evidently separated out the infected portion and submitted it to Zopf. It may have subsequently been borrowed by Vouaux from either ANGUC or B and either lost with much of his own material, or returned to B and destroyed in World War II.

The application of Vouaux's name thus remains uncertain, although the occurrence of branched conidiophores indicates that it cannot be accommodated in *Lichenoconium* as interpreted here.

resinae. — *Lichenoconium resinae* (Sacc. & Berl.) Petr. & Syd. *in* Beih. Repert. Spec. nov. Regni veg. **42**: 436. 1927. — *Coniothyrium resinae* Sacc. & Berl. *in* Atti Ist. venet. Sci., ser. 3, **6**: 739. 1885. — *Epithyrium resinae* (Sacc. & Berl.) Sacc., *in* Saccardo & Trotter, Syll. Fung. **25**: 249. 1931.

This resinicolous species was first described from Italy. Examination of the holotype collection in Saccardo's herbarium (PAD) revealed 180—200 µm diam. pycnidia dehiscing by an irregular breakdown of the upper tissues of the pycnidial wall, ± cylindrical colourless phialides 6—8 × 2.5—3 µm, and globose, smooth, thick-walled, pale brown, simple conidia 2.5—3 µm diam. This fungus is certainly close to *Lichenoconium* but differs in the completely smooth globose conidia and the resinicolous habitat; it is clear that this is the fungus later described as *Biatoridina pinastri* Schczedrova (Bot. Zh. SSSR **49**: 1315. 1964), the conidial state of *Tromera difformis* (Fr.) Arnold. This fungus differs from the conidial state of *T. resinae* (Fr.) Körb. in having dark brown pycnidia.

The generic name *Epithyrium* (Sacc.) Sacc. & Trott. (Syll. Fung. **25**: 249. 1931) can be lectotypified by *E. resinae* (Sacc. & Berl.) Sacc. (B.C. Sutton, *in litt.*) and taken up for the conidial state of *Tromera difformis*.

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NOTE ADDED IN PROOF

While this paper was in press a third collection referrable to *L. cargillianum* and a new host came to light (Ireland: Co. Wicklow, Coolattin House, in apothecia of *Usnea florida* (L.) Web. on *Quercus petraea*, 24 April 1977, *M. R. J. Seaward*, E). In this the apothecia were discoloured brownish and very angular coarsely verrucosse conidia (5.7–7(–7.5) × 4–5.5 μm) produced in pycnidia c. 130 μm diam.

EXPLANATION OF PLATES 21—29

PLATE 21

Figs. A-E. *Lichenoconium boreale* (holotype). — A. Habit on wood, note the irregular ostiole (arrow), ×23. — B. Vertical section of pycnidium, ×390. — C. Vertical section through pycnidial wall showing its prosenplectenchymatous structure and the conidiogenous cells, ×1560. — D. Conidia, ×1560. — E. Conidia as seen by SEM, ×2340.

PLATE 22

Figs. A-E. *Lichenoconium echinosporum* (holotype). — A. Infected thallus of *Heterodea muelleri*, ×18. — B. Vertical section through pycnidial wall showing its pseudoparenchymatous structure and the conidiogenous cells, ×1560. — C. Vertical section of pycnidium, ×390. — D. Conidia, ×1560. — E. Conidia as seen by SEM, ×2340.

PLATE 23

Figs. A-F. *Lichenoconium erodens*. — A-D. Infected thalli of *Hypogymnia physodes*. — A. Young infection spot with several pycnidia, ×17 (holotype). — B. Larger infection spot, ×17 (holotype). — C. Older infection spot from which the centre has fallen away, ×17 (*Christiansen 75.408*). — D. Old infection spot with pycnidia of *L. erodens* and *Phoma* sp. from which the centre has fallen away, ×14 (*hb. Christiansen 63*). — E. Infected thallus of *Evernia prunastri* showing pycnidia (arrow), ×7 (*hb. Christiansen 77*). — F. Infected thallus of *Parmeliopsis ambigua* showing pycnidia (arrow), ×23 (hb. Poelt.). Photographs A-E by M. Skytte Christiansen.

PLATE 24

Figs. A-B. *Lichenoconium erodens* on *Evernia prunasti*. — A. Conidia as seen by SEM, ×1670 (*hb. Christiansen 77*). — B. Conidia, ×1560 (*IMI 205336*).

Figs. C-E. Mixed infection in apothecia of *Parmelia galbina* (*Hale 15246b*). — C. Vertical section of an apothecium with pycnidia of both *L. erodens* (left) and *L. parasiticum* (right), ×350. — D. Vertical section of the *L. erodens* pycnidium in Fig. C showing the small conidia, ×1560. — E. Vertical section of the *L. parasiticum* pycnidium in Fig. C showing the larger conidia, ×1560.

PLATE 25

Figs. A-D. *Lichenoconium lichenicola* (holotype). — A. Vertical section of pycnidium, ×390. — B. Conidia as seen by SEM, ×970. — C. Conidia as seen by SEM, ×1950. — D. Conidia, ×1560.

Figs. E-G. *L. cargillianum*. — E. Vertical section of pycnidium, × 390 (holotype of *Coniothyrium ramalinae*). — F. Conidia, ×1560 (holotype of *Coniothyrium ramalinae*). — G. Conidia, ×1560 (holotype of *Microthelia cargilliana*).

PLATE 26

Figs. A-G. *Lichenoconium parasiticum*, symptoms on infected apothecia and thalli. — A. *Lecanora conizaeoides*, apothecial disc, finally becoming blackened, pycnidium arrowed, × 18 (*IMI 202895*). — B. *Lecanora admontensis* apothecia, pycnidium arrowed, × 24 (*Vezda*). — C. *Squamarina lentigera* apothecia, pycnidium arrowed, × 19 (*Zetterstedt*). — D. *Lecanora rubina* thallus, pyncidium with white arrow, dark brown superficial mycelium with black arrow, × 23 (*hb. Christiansen 108*). — E-F. *Parmelia saxatilis* thallus. — E. Numerous black-bordered infection spots, × 7 (*hb. Christiansen 104*) — F. Single black-bordered infection spot, × 18 (*hb. Christiansen 104*). — G. *Parmelia sulcata* thallus, single central pycnidium, × 23 (*hb. Christiansen 17*). Photograph D by M. Skytte Christiansen.

PLATE 27

Figs. A-D. *Lichenoconium parasiticum*. — A. Vertical section of pycnidium in soralium of *Parmelia sulcata*, × 620 (*Christiansen 12.191*). — B. Conidia on *Lecanora conizaeoides*, × 1560 (*IMI 12680*). — C. Conidia from *Lecanora conizaeoides* as seen by SEM, × 2340 (*Erichsen 198*). — D. Conidia from *Parmelia sulcata* as seen by SEM, × 3110 (*Christiansen 7582*).

Figs. E-H. *Lichenoconium pyxidatae*. — E. Infected podetium of *Cladonia* sp., × 23 (*IMI 142509*). — F. Vertical section of pycnidium, × 390 (holotype). — G. Vertical section through pycnidial wall showing pseudoparenchymatous wall structure and conidiogenous cells, × 1560 (holotype). — H. Conidia, × 1560 (holotype).

PLATE 28

Figs. A-K. *Lichenoconium usneae*. — A. Infected thallus of *Hypogymnia physodes*, × 7 (*Santesson 22663b*). — B. As A but the pycnidia on a swollen lobe, × 18 (*Santesson 22663b*). — C. Infected thallus of *Ramalina subgeniculata*, × 17 (*hb. Christiansen 94*). — D. Infected apothecium of *Ramalina calicaris*, × 17 (*IMI 186833*). — E. Infected apothecium of *Parmelia exasperata*, × 18 (*Santesson 14316c*). — F. Vertical section through pycnidial wall in apothecium of *Parmelia conspersa* showing pseudoparenchymatous structure of wall and conidiogenous cells, × 1560 (lectotype of *Coniothyrium jaapii*). — G. Vertical section through pycnidium in *Usnea filipendula* aggr. apothecium, × 620 (isotype). — H. Conidia from *Parmelia olivacea* apothecium as seen by SEM, × 2730 (*Santesson 14169c*). — I. Conidia from *Ramalina calicaris* apothecium as seen by SEM, × 2730 (*IMI 186833*) — J. Vertical section through pycnidial wall in *Usnea filipendula* aggr. apothecium showing pseudoparenchymatous wall structure and conidiogenous cells, × 1560 (isotype). — K. Conidia from *Usnea filipendula* aggr. apothecium, × 1560 (isotype). Photograph C by M. Skytte Christiansen.

PLATE 29

Figs. A-C. *Lichenoconium pertusariicola* on thallus of *Pertusaria pertusa*. — A. Infected thallus showing pycnidia (arrow), × 18 (*IMI 166296*). — B. Vertical section of pycnidial wall showing the hyaline wall cells and pigmented conidiogenous cells, × 1560 (*IMI 186240*). — C. Conidia, × 1560 (*IMI 186240*).

Fig. D. *Lichenoconium xanthoriae* on apothecia of *Xanthoria polycarpa*, pycnidium arrowed, × 17 (holotype).

Fig. E. *Lichenoconium pertusariicola* conidia from *Pertusaria leioplaca* thallus as seen by SEM, × 2340 (*Bowen*, 1975).

Fig. F-J. *Lichenoconium xanthoriae*. — F-H. On *Xanthoria polycarpa* apothecia. — F. Conidia, × 1560 (holotype). — G. Conidia as seen by SEM, × 780 (holotype). — H. Conidia as seen by SEM, × 3110 (holotype). — I. On *Parmelia olivacea* apothecium, pycnidium arrowed, × 18 (*Alm*, 1952 p.p.). — J. On *Cetraria sepincola* apothecium, pycnidium arrowed, × 23 (*IMI 189905*).

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NOTES ON THE GENUS PSATHYRELLA—V

The sections Ammophilae, Bipellis and Subatratae

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(With 52 Text-figures)

The treatment of subgenus *Psathyrella* is rounded off with descriptions of and observations on *Psathyrella ammophila*, *P. bipellis* and *P. conopilus*, each the type species and sole representative in Europe of respectively section *Ammophilae sect. nov.*, section *Bipellis* and section *Subatratae*.

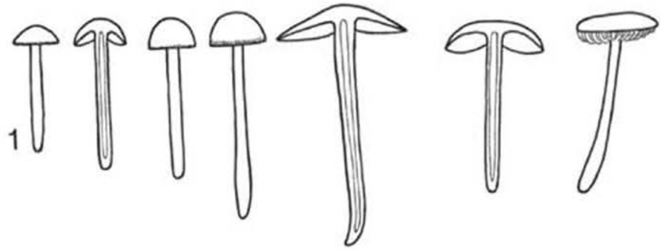
Having dealt with sections *Atomatae* (Romagn.) ex Singer and *Psathyrella* emend. Kits van Wav. of *Psathyrella* subgenus *Psathyrella* in two previous papers (Kits van Waveren 1972: 23—54 and 1976: 345—405), in the present paper we are rounding off our treatment of this subgenus by describing and discussing the remaining three species of the subgenus *Psathyrella*, each of which is both sole European representative and type species of a separate section of the subgenus: *P. ammophila* (Dur. & Lév.) P. D. Orton for which we propose a new section, section *Ammophilae*, *P. bipellis* of section *Bipellis* Malençon & Romagn. and *P. conopilus* of section *Subatratae* (Romagn.) ex Singer.

For our methods of examining the pleuro- and cheilocystidia, the shape, size and colours of the spores, the basidia and the pigmentation of the hymenophoral trama, the reader is referred to our previous papers (Kits van Waveren 1968: 132; 1971a: 249, and 1972: 24). As in our previous papers spore measurements are given both as a range and as a mean value added between brackets. Whenever spores were measured for this purpose it was always 20 of the darkest (=ripest) spores, found on a gill, that were measured. For the description of the colours of the carpophores, spores and pigmentation of hymenophoral trama we used 'Munsell Soil Color Charts' edition 1971 (abbreviated: M.).

It is again assumed that Romagnesi wrote the chapter on the genus *Drosophila* in the 'Flore analytique' (Kühn. & Romagn., 1953), which explains why only his name is quoted when our text refers to this chapter.

For reasons given in our earlier paper (Kits van Waveren 1976: 346) in the descriptions of the species we have omitted the structures and the pigmentation of the various layers of the flesh of the cap. For our warning against misinterpretation of the misleading colours of seemingly fresh caps and their flesh due to the early and not realized onset of the process of drying out, also see our previous paper (1976: 346).

In our descriptions we continued to call the pleurocystidioid cells on the gill edge



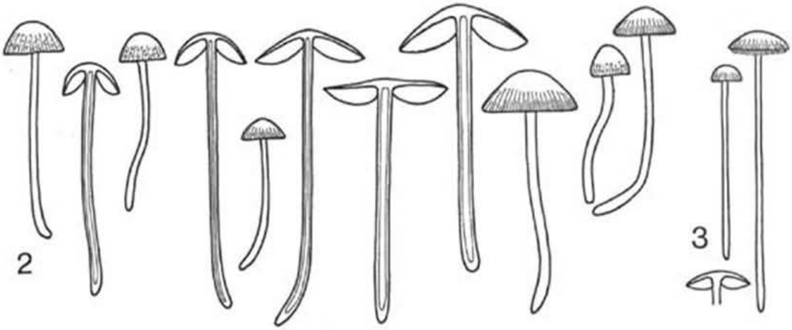


Fig. 1. *Psathyrella ammophila*, 7 Sept. 1965. — Habit sketch (× ½).
Figs. 2, 3. *Psathyrella bipellis*. — Habit sketches (× ½). — 2. 16 Nov. 1976. — 3. 24 July 1966.

'cheilocystidia', and the other type of cells 'spheropedunculate cells', while as far as possible we estimated the ratio between the two types of cells as they occur on the sterile gill edge (Kits van Waveren 1976: 348).

In the list of collections the author's name is abbreviated to E.K.v.W.

We are greatly indebted to Professor A. H. Smith for lending us five of his collections of *P. arenulina* (Peck) A. H. Smith.

Psathyrella section **Ammophilae** Kits van Wav., *sect. nov.*

Carpophora solitaria, in dunarum arenis frequentia. Pileus majusculus, subcarnosus, haud vel vix striatus, sordide brunneus, hygrophanus. Velum manifestum tametsi fugax. Lamellae ventricosae, obscure purpureo-brunneae, acie albae. Stipes arrhizus, parte inferiore atque in arenum insertus. Sporae in cumulo purpureo-atratae, 10–14 × 6–7 μm, poro germinativo praeditae. Basidia 4-sporigera. Pleurocystidia exigua, magna. Cheilocystidia pleurocystidiis similia, vulgo exigua. Cellulae spheropedunculatae clavataeque crebrae. Trama lamellarum colorata. — Species typica: *Psathyrella ammophila* (Dur. & Lév.) P. D. Orton.

Carpophores solitary in shifting coastal dunes; cap medium sized, rather fleshy, not or scarcely striate, sordid brown, hygrophanous; veil distinct but fugacious; gills ventricose, dark purplish brown with white edge; stem not rooting but lower half or third buried in the sand, spore print purplish black; spores 10—14×6—7 μm with distinct germ pore; basidia 4-spored; pleurocystidia scarce, large; cheilocystidia normally scarce, similar to pleurocystidia; spheropedunculate and clavate cells very numerous; hymenophoral trama coloured. — Type species: *Psathyrella ammophila* (Dur. & Lév.) P. D. Orton.

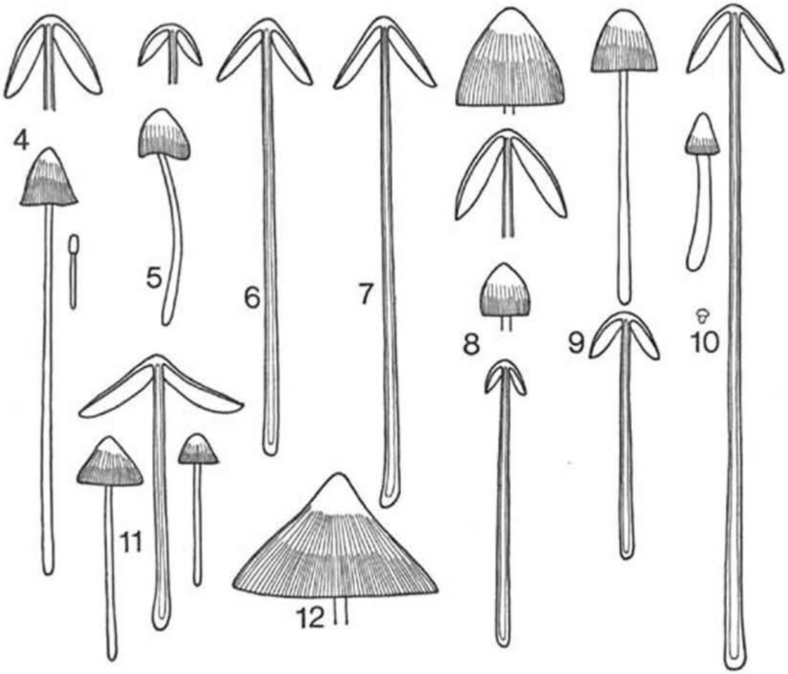
For discussion see under *P. ammophila* (p. 000).

PSATHYRELLA AMMOPHILA (Dur. & Lév.) P. D. Orton—Figs. 1, 13—29

Agaricus ammophilus Dur. & Lév., Explor. sc. Alg. **14**: 1868, pl. 31 fig. 8. 1848. — *Psilocybe ammophila* (Fr.) Gill., Hym. Fr.: 587. 1878. — *Psathyra ammophila* (Dur. & Lév.) Quél. *in* Bull. Soc. bot. Fr. **26**: 52. '1879' [1880]. — *Drosophila fatua* var. *ammophila* (Dur. & Lév,) Quél., Enchir. Fung.: 117. 1886. — *Drosophila ammophila* (Dur. & Lév.) Quél., Fl. mycol. Fr.: 62. 1888. — *Deconica ammophila* (Dur. & Lév.) Morgan *in* J. Mycol. **13**: 145. 1907. — *Hypholoma ammophilum* (Dur. & Lév.) Bigeard & Guillemin, Flore Champ. sup. Fr.: 345. 1909.

Psilocybe ammophila var. *ecaudata* Maire *in* Bull. Soc. bot. Fr. **56**: 279. '1909' [1911)].

Psilocybe subammophila Cleland *in* Trans. Proc. Roy. Soc. South Austr. **51**: 306. 1927.



Figs. 4—12. *Psathyrella conopilus*. — Habit sketches (×½). — 4. 7 Oct. 1961. — 5. 8 Nov. 1962. — 6. 22 Sept. 1964. — 7. 23 Oct. 1965. — 8. 8 Oct. 1966. — 9. 11 Nov. 1967. — 10. 15 Nov. 1968. — 11. 13 July 1968. — 12. 3 Oct. 1975.

Agaricus arenulinus Peck *in* Rep. N.Y. States Mus. **30**: 42. 1878. — *Psilocybe arenulina* (Peck) Sacc., Syll. Fung. **5**: 1–57. 1887. — *Psathyrella arenulina* (Peck) A. H. Smith *in* Mem. N.Y. bot. Gdn. **24**: 276. 1972.

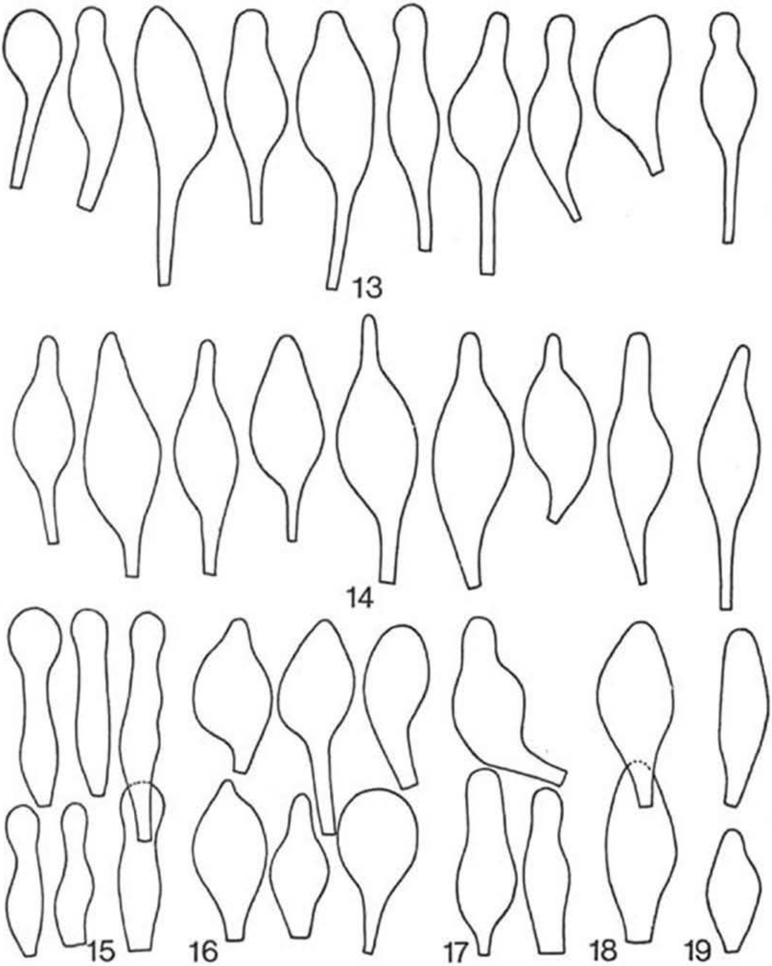
SELECTED DESCRIPTIONS AND ILLUSTRATIONS.—Cooke, Ill. Brit. Fungi: pl. 606B/599. 1884–1886 (as *Agaricus ammophilus*); Bresadola, Iconogr. mycol. **18**: pl. 857. 1931 (as *Psilocybe ammophila*); J. E. Lange, Fl. agar. dan. **4**: 82, pl. 148B. 1939 (as *Psilocybe ammophila*); Kühn. & Romagn., Fl. anal.: 358. 1953 (as *Drosophila ammophila*); Singer *in* Mycopath. Mycol. appl. **34**: 132. 1968; Bon *in* Bull. Soc. mycol. Fr. **86**: 108. 1970 (as *Drosophila ammophila*); Malençon & Bertault, Fl. champ. sup. Maroc **1**: 179. 1970 (as *Drosophila ammophila*); Michael/Hennig **4**: 276, pl. 262. 1967 (as *Deconica ammophila*).

CHIEF CHARACTERISTICS.—Carpophores solitary to gregarious in coastal, shifting foredunes; cap 15–40 mm in diam., from hemispherical paraboloid to convex or plane with deflexed margin, not or only faintly striate, rather fleshy, from reddish brown to dark sordid brown, hygrophanous, without pink shades, rugulose; with distinct but fugacious marginal veil; gills strongly ventricose, dark purplish-brownish grey with white edge; stem 40—70 × 2—3 mm, not rooting but lower part sunk in the sand; spore print purplish black; spores 10.5—13.5 × 6.5—7 μm with central germ pore; pleurocystidia normally very scarce and large, size and shape very variable, 40—70 × 12.5—22.5 μm; spheropedunculate and clavate cells at gill edge normally very numerous and densely packed, intermixed with usually very few but sometimes more or even many cheilocystidia, similar to pleurocystidia; hymenophoral trama coloured.

MACROSCOPIC CHARACTERS.—Cap 15–40 mm in diam., 8–10 mm high, in early stages hemispherical to paraboloid, later spreading to convex with deflexed margin, finally plane at centre with deflexed or plane margin, sometimes slightly depressed at centre, without umbo, with its margin not or only faintly striate, rather fleshy and firm, at first distinctly reddish brown (M. 5 YR 3/3) but soon very dark sordid brown (M. 7.5 YR 3/2) or just dark sordid brown (M. 7.5 YR 4/2) with peripheral half having a slightly different hue (M. 10 YR 3/3, 3/4), hygrophanous, rapidly dehydrating from margin to centre and colour becoming dark brown (M. 10 YR 3/3-3/4, 4/3) at centre, paler (M. 10 YR 5/3, 6/3; colour of wet white sand) in peripheral half, finally yellowish brown (M. 10 YR 7/4, 7/6) at centre and pale brown (M. 10 YR 6/3, 7/3) at periphery, without pink shades, not micaceous, slightly rugulose.

Veil in early stages very distinct, forming a dense covering of minute white fibrils, isolated or in small groups and networks, on the 2.5–5 mm wide marginal zone of cap, rendering this zone whitish, rarely locally slightly appendiculate, fugacious but later often still forming some isolated fibrils or small networks of fibrils on 5–7 mm wide marginal zone, leaving scattered fibrils on mature stem, but in early and very early stages sometimes forming a woolly covering of the stem.

Gills in early stages 2–3 mm broad and only slightly ventricose, in peripheral half pale brownish grey (M. 10 YR 6/2), in basal part slightly browner (M. 10 YR 5/2), later 4–6 mm broad, increasingly and finally strongly ventricose, protruding under margin of expanding cap, broadly adnate, rather distant, at first still conspicuously brown (M. 10 YR 5/4) at base but greyer and more purplish grey towards edge, finally dark purplish brownish grey (M. 5 YR 4/2, 3/2) and slightly browner towards base; edge white, very rarely red, and minutely fimbriate. Trama of 'washed' gills under binocular lens in water ochre brown (M. 7.5 YR 6/4–6/6) along base, with pigmented parallel strands running from base to about mid-way or somewhat further towards edge of gill and of same hue as trama at base but becoming paler towards edge; colour between strands and in peripheral 1/3 of the gills very pale greyish brown (M. 10 YR 7/2). Colour of 'washed' gills in NH_4OH 10% practically the same, scarcely more reddish brown (M. 5 YR 6/4 at base), strands paler and colour between strands and in peripheral part M. 7.5 YR 7/2 or 5 YR 7/2; colour in KOH 5% scarcely different from that in NH_4OH 10% (slightly more towards 5 YR 5/3 at base).



Figs. 13–19. *Psathyrella ammophila*. — Pleurocystidiograms (× 575). — 13. 15 Oct. 1972. — 14. 7 Sept. 1965. — 15. 10 Oct. 1965. — 16. 7 June 1965. — 17. 22 Oct. 1965. — 18. 29 April 1952. — 19 July 1955.

Stem 40–70 mm long, hollow; its upper 2/3–3/4 part 2–3 mm thick, cylindrical, sordid white to pale yellowish brown, minutely fibrous-striate, with apex pruinose and usually grooved; its lower 1/4–1/3 part 3–5 mm thick, sunk deeply in the sand, not really rooting, seemingly somewhat clavate or fusiform as a result of adhering sand, with subobtuse end.

Flesh of cap rather thick, 2–4 mm in centre, 1.5–2 mm half-way margin of cap, dark brown (M. 10 YR 3/4), of stem whitish.

Taste and smell not distinctive.

Spore print purplish black.

MICROSCOPIC CHARACTERS.—Spores ellipsoid-amygdaliform, (9.9–)10.8–13.5 × 6.3–7.1(–8.1) μm (averages 10.8–12.6 × 6.6–7.4 μm), in water dark reddish brown (M. 2.5 YR 3/4), in NH_4OH 10% darker, dusky red to very dark reddish brown (M. 2.5 YR 3/2; 5 YR 3/2, 3/3), in KOH 5% very dark greyish brown (M. 10 YR 3/2), opaque to subopaque, with large, 1.5–2 μm wide, central, subtruncate to truncate apical germ pore, with relatively small hilar appendix.

Basidia 22.5–37.5 × 10–12.5 μm, 4-spored.

Pleurocystidia (30–)40–70(–75) × (10–)12.5–22.5(–27.5) μm, normally very scarce, scattered, of variable size and shape, usually subfusiform, ventricose-fusiform or ventricose-sublageniform, often with short or somewhat longer subcylindrical neck, sometimes clavate, sometimes with fairly long stalk, thin-walled, colourless.

Spheropedunculate and clavate cells 20–37.5(–40) × 10–22.5(–30) μm, as a rule very numerous and densely packed, rendering gill edge sterile, rather large and mostly with fairly broad stalk, normally intermixed with only an extremely small, rarely a fair to even large number of cheilocystidia, 25–55(–70) × 10–17.5(–20) μm, of the same very variable shape as the pleurocystidia, fusiform, narrowly to very broadly ventricose-fusiform, subfusiform, ventricose-lageniform or sublageniform, subutriform, subcylindrical, some with elongated neck or subcapitate etc., practically absent near margin of cap in most collections; all marginal cells thin-walled, colourless and without crystals or mucoid deposits.

Pigmentation of hymenophoral trama under microscope ('washed' gill mounted in NH_4OH 10%) sordid brownish at base of gill, paler towards edge, from membranal pigment; at base of gill a few thickened yellowish hyphal septa and very few encrustations present.

Cuticle of cap cellular, 2–4 cells deep; its cells 20–48 μm in diam., hyaline, thin-walled.

Clamps present.

HABITAT.—Among or near grasses (particularly *Ammophila*) on shifting coastal foredunes, May—October, common.

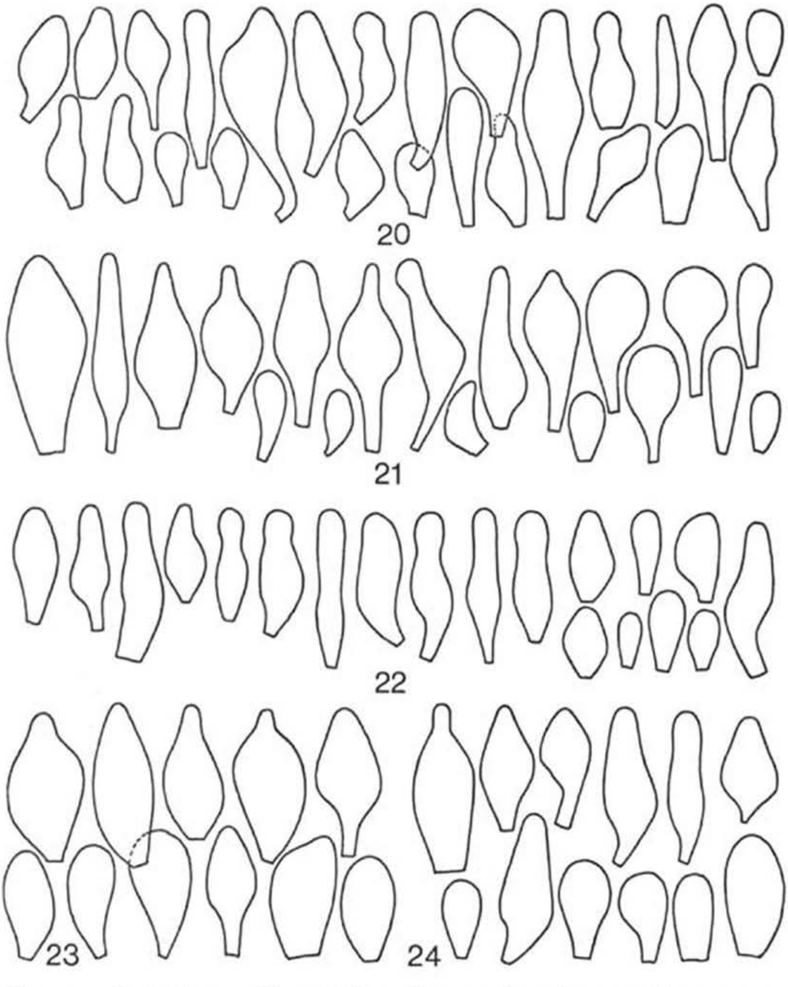
COLLECTIONS EXAMINED.—NETHERLANDS: prov. Friesland, Isl. of Terschelling, July 1955, *P. B. Jansen* (L); Isl. of Schiermonnikoog, July 1956, *J. Daams* (L); Isl. of Ameland, 11 June 1958, *K. Bakker* (L); prov. Noord-Holland, Isl. of Texel, 7 June 1965, *C. Bas* (L); prov. Zuid-Holland, Wassenaar, 10 Oct. 1965, *C. den Hartog* (L); Oost Voorne, 22 Oct. 1962, *A. F. M. Reijnders* (L); prov. Zeeland, Zuid-Beveland, 29 Apr. 1952, *W. G. Beeftink* (L).

GREAT BRITAIN: Devonshire, Minehead, 5 Sept. 1960, *E.K.v.W.* (L); Lancashire, Ainsdale Sands near Formby, 7 Sept. 1965, *E.K.v.W.* (L).

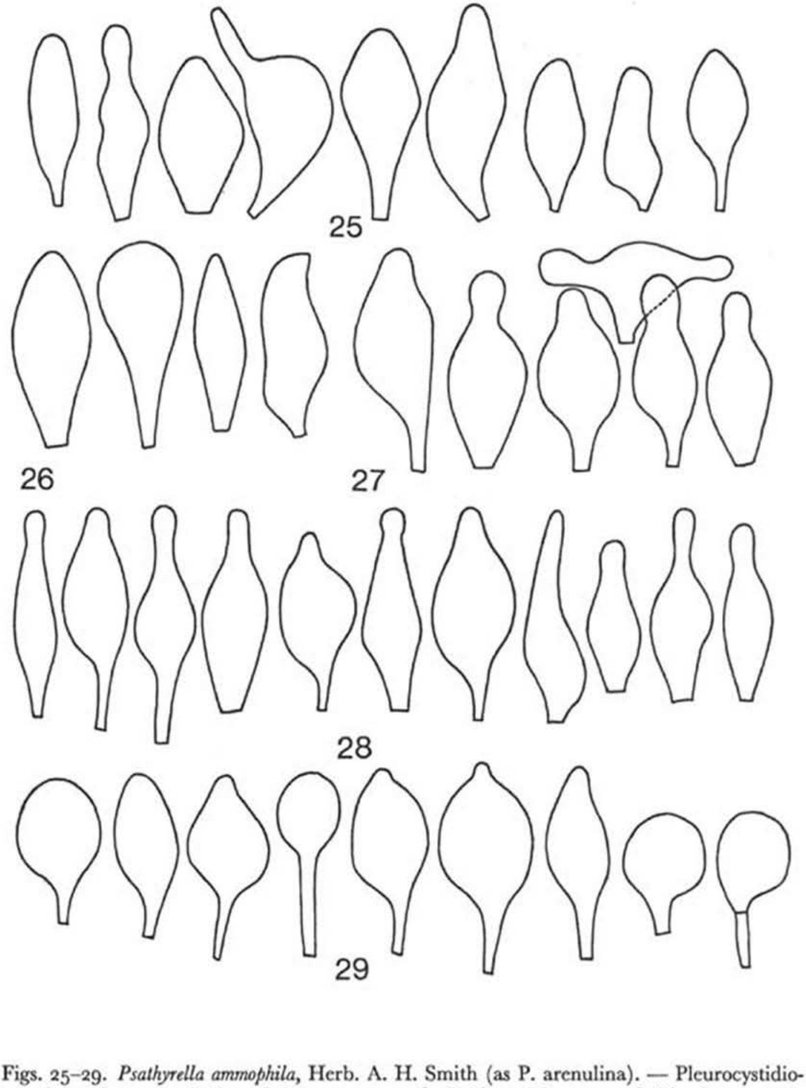
FRANCE: dép. Pas-de-Calais, Tardinghen, 15 Oct. 1972, *D. Tjallingii-Beukers* (L).

ALGIERS: Laghouat, 1903, *N. Patouillard* (PC).

The above description of the macroscopic characters is based largely on the very rich collection of some 20 specimens, including all stages, of 7 September 1965 (Ainsdale Sands, Formby, Great Britain), which was collected and described immediately afterwards while still in the fresh stage. One young specimen of this collection had a very distinct red gill edge.



Figs. 20–24. *Psathyrella ammophila*. — Cheilocystidiograms (× 575). — 20. 15 Oct. 1972. — 21. 7 Sept. 1965. — 22. 10 Oct. 1965. — 23. 7 June 1965. — 24. 22 Oct. 1962.



Figs. 25–29. *Psathyrella ammophila*, Herb. A. H. Smith (as P. arenulina). — Pleurocystidiograms (× 575). — 25. *Bailey*, 28 July 1951. — 26. *Smith 21861*. — 27. *Smith 36129*. — 28. *Smith 51187*. — 29. *Smith 4724*.

The macroscopic characters of this species are remarkably consistent, all dried specimens looking exactly the same. This is in contrast to the features of the pleurocystidia and the marginal cells of the gill, which vary a great deal from one collection to another.

Romagnesi (1953: 358) quite rightly states that the cystidia are: 'éparses, mais volumineuses'. Of each of our 10 collections of *P. ammophila* we isolated a gill, then 'washed' it, carefully separated its edge from its face and disrupted the facial part into a large number of small pieces, which were crushed under a coverslip by tapping it. In this way we could be sure that if cystidia were to be found in the facial part, they would be pleurocystidia. In our 10 collections we found per gill resp. 0, 1, 2, 3, 5, 7, 11, 12, ± 15 pleurocystidia; in only one collection (10 Oct. 1965) were they slightly more numerous, scattered. The pleurocystidiograms clearly show the great variability in size and shape of these cells.

Although Romagnesi in the 'Flore analytique' places *P. ammophila* in the *Microrrhizae* ('Stipe ± longuement radicant') the stem of this species is not really rooting. Romagnesi himself, in describing the species, does not speak of a 'root', stating merely that the stem is 'longuement enfoncé dans le sable.' The original picture given by Durieu & Léveillée does not depict a pseudorrhiza either. J. E. Lange (1939: 82) in his description puts the word 'root' between inverted commas, indicating that he also does not regard the stem as rooting, and his excellent pictures (Fig. 148B) clearly show the absence of a real pseudorrhiza, the basal end of the stem being depicted as very obtuse. Cooke's plate 606B/599 (1884—1886) does not show a real pseudorrhiza nor does Bresadola's plate 857. Bon (1970: 108) does not mention the presence of a pseudorrhiza and even calls the stem 'parfois même bulbeux'. Singer (1968: 132) describes the stem as usually with rounded base, more rarely with attenuated base.

Macroscopically the specimens of the Wassenaar collection (10 Oct. 1965) were fully identical with those of all our other collections but microscopically they differed distinctly from these: (i) the pleurocystidia were fairly numerous; (ii) they were both utriform and strikingly uniform (see Fig. 15); (iii) the cellular lining of the gill edge consisted chiefly of densely packed and rather small cheilocystidia (shape very variable) intermixed with only a small number of rather inconspicuous spheropedunculate and clavate cells: (iv) the germ pore was indistinct and small. For a long time we hesitated whether to describe this collection as a new form of *P. ammophila*, but in the end refrained because a macroscopic description was lacking.

TAXONOMIC POSITION OF PSATHYRELLA AMMOPHILA.—In a previous paper (1976: 350) we strongly advocated and also adopted Romagnesi's concept of the subgenus *Psathyrella*. It was also adopted by Singer (1975: 504) who rejected that part of Smith's (1972: 30) subdivision of the genus *Psathyrella* in which the subgenera *Psathyrella* and *Pannucia* are separated on account of the degree of development of the veil rather than the size and shape of the spores and the basidia. *Psathyrella ammophila*, because of its large spores and short, thickset basidia, obviously belongs to *Psathyrella* subgenus *Psathyrella* ss. Romagnesi. Because of its habit, fairly large, rather fleshy and non-striate cap, its normally sparse and voluminous pleurocystidia and its habitat it cannot possibly be ranked with the species of section *Atomatae*; for the same reasons and also because of the absence of a pseudorrhiza it cannot be ranked with the species of section *Psathyrella* either. Therefore we have established a separate section for this species: section *Ammophilae*.

PSATHYRELLA AMMOPHILA VERSUS P. ARENULINA.—Smith (1972: 343, 276) in his observations on both *P. ammophila* (of which species he examined only one collection) and *P. arenulina* (17 collections examined) discusses the relationship and possible conspecifity of the two species and concludes that 'a critical restudy of both should be made'. Such a restudy we offer below.

From Smith's descriptions and observations it is clear that if there should be any difference at all between the two species it would lie in the presence or absence of pleurocystidia, the spore sizes, the presence or absence of a veil, and the thickness of the flesh of the cap.

Smith found the pleurocystidia to be scattered in his collection of *P. ammophila*, and absent in all of his 17 collections of *P. arenulina*. This is why at the very beginning of his key to the species of subgenus *Psathyrella*, *P. arenulina* keys out with section *Subatratae* (pleurocystidia absent), whereas *P. ammophila* finds itself in section *Psathyrella* and, because its spores are slightly larger than those of the species of subsection *Mesosporae*, within that section in subsection *Psathyrella*.

At our request Dr. A. H. Smith very kindly sent us material of five of his collections of *P. arenulina* for examination. With the same technique as described above (p. 199) we checked the presence or absence of pleurocystidia. On a gill of the collection marked '*Bailey 7–28–1951*' (see Smith 1972: 277) we found 11 pleurocystidia, very variable in both shape and size, of collection *Smith 21861* only four (also very variable) of collection *Smith 36129* six (utriform and measuring 45—57 × 18—22 μm), of collection *Smith 51187* a fairly large number (our cystidiogram alone shows 15 cells, all rather uniform, sublageniform-subfusiform and at the same time subcapitate, 45—60 × 12—22 μm), and of collection *Smith 4724* ten (both in shape and size very variable, strikingly ventricose and pedicellate, 37—55 × 17—27 μm). In all the collections the marginal cells, studied separately under another coverslip, were quite different, generally rather large, clavate to spheropedunculate and intermixed with a fair number of scattered cheilocystidia of varying sizes and shapes. In conclusion we believe that the gills of all five specimens labelled *P. arenulina* that we studied bear pleurocystidia, as they do in *P. ammophila*.

As for the spore sizes in the 10 collections of *P. ammophila* we studied we found them to differ from one collection to another. We found the smallest spores (9.9—11.7 × 6.3—7.2 μm) in the collection of 29 April 1952, the largest (11.7—13.5 × 7.2—7.7 μm) in our collection of 5 Sept. 1960, the mean values in our 10 collections being 10.8—12.6 × 6.6—7.4 μm (of each collection 20 spores measured). These figures are slightly larger than the figures 10—11 × 6—7 μm, 10—11 × 7 μm and 8.7—11.7 ×

5.8—7.3 µm given by resp. Kühner & Romagnesi (1953: 358), Moser (1967: 214) and Singer (1968: 132), and agree with the figures 10—15×6—8 µm, 10—12.4×6.2—7.2 µm and 9—14×6—8 µm given by resp. Bresadola (1931: Pl. 857), Malençon & Bertault (1970: 179) and Smith (1972: 343).

Singer (1968: 321) comments on the spore size. Quoting Andersson's (1950: 33) figures of 10—12—14(—16)×6.5—8 µm and Pilát's (1951: 364), which go up to 12 µm long for the spore size, Singer states that according to his own findings on Netherlands' material the spores are 11.5—13 µm long, figures which fully agree with our own. Singer believes therefore that in European material the spores often reach a larger size than in the American material. Our figures for the *P. arenulina* material received from Dr. Smith are (9—)9.9—13.5(—14.4)×(5.4—)5.9—7.2 µm (mean values 10.5—12.4×6.1—6.8 µm) those of Smith himself 9—12(—12.5)×5.6 µm, and those of Murrill (1923: 8) 10—12×5—6 µm. All these figures, both in the literature and in our own measurements of 10 collections of *P. ammophila* and 5 of *P. arenulina* are sufficient to show that there is no significant difference between the spore sizes of what is called *P. arenulina* and *P. ammophila*.

As for the veil, it is thin, very fugacious and as a result apparently often overlooked and also evidently variable in *P. ammophila*. Except for Kühner & Romagnesi (1953: 358), Moser (1967: 214), Smith (1972: 343), and Malençon & Bertault (1970: 343) none of the numerous other authors — among whom Bon (1970: 108), Maire (1911: 279), Andersson (1950: 33), J. E. Lange (1939: 82), Bresadola (1931: Pl. 857)—who gave either short or more elaborate descriptions of this remarkable species mentioned the presence of a veil or velar remnants on the cap, and Singer (1968: 132) even specifically stated that the cap is without remnants of a veil. Smith (1972: 277) states that he has not observed a veil in the Michigan collections of *P. arenulina*, admitting, however, that very few buttons were found. In the one and only collection Smith was able to examine of *P. ammophila* the margin was found to be thinly fibrillose at first but soon naked.

In most of our ten collections of *P. ammophila* the description of the macroscopic characters was either lacking or too short and incomplete, but in four the presence of a veil was mentioned (29 April 1952: 'cobweb velar remnants at margin'; 22 Oct. 1962: 'much velar tissue, in places slightly appendiculate scattered velar fibres at and even up to some distance from the margin in some mature specimens'; 7 June 1965: 'some fresh specimens with remains of an annulus'; for the rich collection of 7 Sept. 1965 see our description above).

The veil, as shown in the above data obviously being so little developed and so easily overlooked in *P. ammophila*, warrants the conclusion that from Smith's data it is not sufficiently justifiable to conclude that *P. ammophila* does and *P. arenulina* does not have a veil.

Although, as Smith correctly states, the context of the caps in *P. ammophila* is thick and fleshy, these caps are fragile. Of *P. arenulina* Smith calls the caps even 'very fragile', but the context thin. Unfortunately figures for the thickness of the flesh in both species are not given. Curiously enough Smith does not use this presumed difference in thickness of the flesh in distinguishing the two species. Macroscopically the dried material of *P. arenulina* we received from Smith was identical in every respect with that of our collections of *P. ammophila*, also with regard to the thickness of the caps, so that we believe this difference to be of no importance.

Murrill (1923: 8) saw the type specimens of Peck's *A. arenulinus* and noticed that Peck had written on the sheet 'perhaps *ammophilus*'.

PSATHYRELLA AMMOPHILA VERSUS P. SUBAMMOPHILA.—Cleland (1927: 306) states that his *P. subammophila* differs from *P. ammophila* by its longer stem (75 mm), adnate and not subdecurrent gills, slightly narrower spores (×5.5—6 μm) and its location in 'sandy agricultural land'. In our description of *P. ammophila* we state that the length of the stem may go up to 70 mm, that the gills are broadly adnate, that the width of the spores is 6.3—7.1 μm, and that the habitat is shifting coastal foredunes. We are not impressed by the narrowness of the spores as reported by Cleland for his *P. arenulina* since Bon (1970: 108) finds the width of the spores in one of his collections to be 5—6 μm, and Singer (1968: 132) mentions for the width 5.8—7.3 μm, for European material even down to 4 μm. Finally Cleland found his species 'in sandy soil near Kinchina, Henley Beach' (Australia). From these data we conclude that *P. subammophila* and *P. ammophila* must be conspecific.

PSATHYRELLA section BIPELLIS Malençon & Romagnesi

Psathyrella section *Bipellis* Malençon & Romagnesi *in* Bull. Soc. mycol. Fr. **69**: 117. 1953.

PSATHYRELLA BIPELLIS (Quél.) A. H. Smith—Figs. 2, 3, 30—46

Psathyra bipellis Quél. *in* C.r. Ass. Franç. Av. Sci. **12**: 501. 1884. — *Drosophila bipellis* (Quél.) Quél., Fl. mycol.: **62**. 1888. — *Psathyrella bipellis* (Quél.) A. H. Smith *in* J. Elisha Mitchell sci. Soc. **62**: 187. 1946.

Psathyra barlae Bres., Fung. Trid. **1**: 84, pl. 91. 1887. — *Psathyrella barlae* (Bres.) A. H. Smith *in* Contr. Univ. Mich. Herb. **5**: 39. 1941.

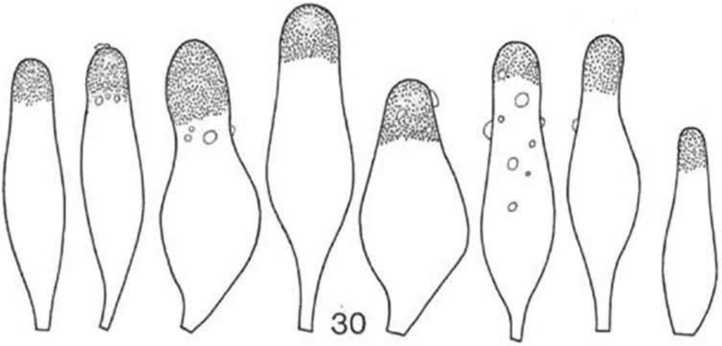
? *Agaricus canofaciens* Cooke *in* Grevillea **14**: 1. 1885; Ill. Brit. Fungi, pl. 595/621. 1884–1886; Handb. Brit. Fungi 2nd Ed.: 209. 1887.

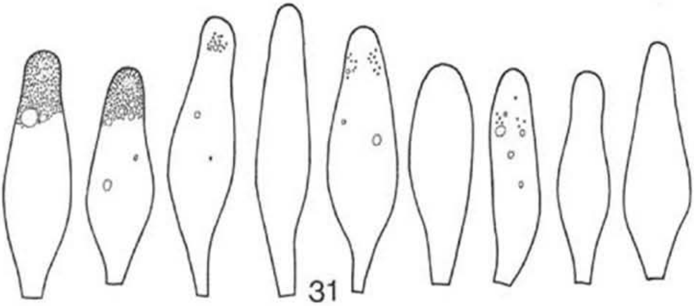
? *Gymnochilus roseolus* Clem. *in* Bot. Survey Nebraska **4**: 231. 1896. — *Psathyra roseola* (Clem.) Sacc. *in* Syll. Fung. **14**: 154. 1899.

MISAPPLIED NAMES.—*Agaricus atro-rufus* Schaeff. ss. Cooke, Ill. Brit. Fungi pl. 602/571. 1884–1886. — *Psathyra corrugis* (Pers. ex Fr.) Quél. ss. Ricken, Blätterp.: 257. 1913.

SELECTED DESCRIPTIONS AND ILLUSTRATIONS.—Cooke, Ill. Brit. Fungi: pl. 602/571. 1884-1886 (as *Agaricus atro-rufus*); Ricken, Blätterp.: 257, pl. 67 fig. 3. 1913 (as *Psathyra corrugis*); Bresadola, Icon. mycol. **18**: pl. 870. 1931 (as *Psathyra barlae*); A. H. Smith *in* Contr. Univ. Mich. Herb. **5**: 39. 1941 (as *Psathyrella barlae*); Malenç. & Romagn. *in* Bull. Soc. mycol. Fr. **69**: 122–126, pl. 1. 1953 (as *Drosophila bipellis* and *Psathyra barlae*); Kühn &. Romagn., Fl. anal.: 354. 1953 (as *D. bipellis*); Romagn., Nouvel Atlas champ. **3**: pl. 204 B. 1961 (as *D. bipellis*); Moser *in* Gams, Kl. Kryptog Fl. **2**/b2, 3. Aufl.: 213. 1967; Hongo *in* Trans. mycol. Soc. Japan **9**: 18. 1968; A. H. Smith *in* Mem. N.Y. bot. Gdn **24**: 103. 1972 (as *Psathyrella barlae*); Malençon & Bertault, Fl. Champ. sup. Maroc **1**: 182. 1970 (as *D. bipellis*).

CHIEF CHARACTERISTICS.—Carpophores solitary; cap from conico-paraboloid to convex, 10–40 mm in diam., very dark purple to purplish red, striate, hygrophanous,





Figs. 30, 31. *Psathyrella bipellis.* — Pleurocystidiograms (×575). — 30. Epse, 16 June 1974. — 31. Bathmen, 16 June 1974.

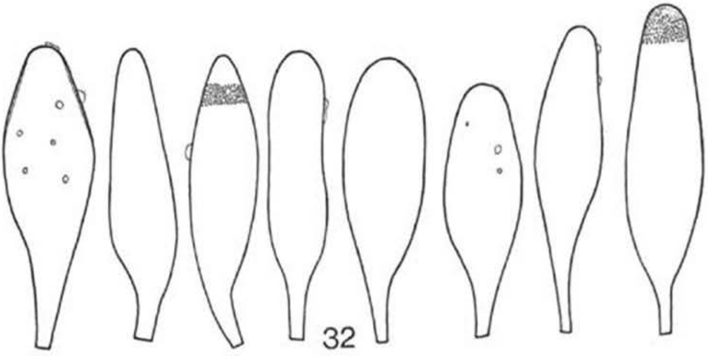
drying to pale reddish or pinkish brown, rugulose, with distinct but fugacious, white veil; gills ventricose, dark purplish red or purplish brown with white edge; stem 45–95 × 1.5–5 mm, not rooting, sordid white with some pink, pinkish brown or purplish; flesh of cap dark vinaceous brown, flesh of stem pale purplish pink; spore print black; spores 12.5–15.5 × 7–8 μm, with germ pore; pleurocystidia abundant, varying from utriform to lanceolate fusiform, 52–95 × 12–30 μm, often with guttulate contents in upper part; cheilocystidia densely packed and similar to pleurocystidia but smaller, intermixed with a small number of small clavate cells; hymenophoral trama coloured.

MACROSCOPIC CHARACTERS.—Cap in the early stages conico-paraboloid, soon conico-convex, in the end almost to quite plane with slightly deflexed margin, 10–40 mm in diam., striate up to 1/3–1/2(–3/4) from margin upwards, very dark, in very young specimens blackish, purple to purplish red (M. 10 R 2.5/1, 2.5/2, 3/2, 2/2; 2.5 YR 2/2, 2/4, 2.5/2, 2.5/4, 3/2), marginal area dusky red (M. 10 R 3/3), at margin itself often reddish (M. 10 R 4/4, 5/4); hygrophanous, drying out from centre towards margin via vinaceous red (M. 10 R 4/4; 2.5 YR 5/4) and reddish brown (M. 2.5 YR 4/4, 5/4) to pale reddish or pinkish brown. (M. 5 YR 6/4), slightly micaceous, slightly to moderately rugulose.

Veil distinct, forming small and rather dense white networks, in very young and young specimens densely covering marginal zone of cap and very numerous to numerous up to 1/2–3/4 from margin upwards and sometimes in places even appendiculate, fugacious.

Gills 3–6 mm broad, moderately crowded, ventricose, usually protruding below margin of cap, narrowly to moderately broadly adnate, dark purplish red or purplish brown (M. 10 R 3/3; 2.5 YR 3/2, 3/4, 2.5/4; 5 YR 3/2), towards edge and in older specimens purplish grey-brown (M. 2.5 YR 4/2; 5 YR 4/2), with white, fimbriate edge. Trama of 'washed' gills under binocular lens rather strongly pigmented; colour when mounted in water or NH_4OH 10% reddish brown (M. 5 YR 5/3) from base to about half-way edge, then paler and via light reddish brown (M. 5 YR 6/3) to very pale greyish brown (M. 10 YR 7/2) near edge, or in these same areas from just brown (M. 7.5 YR 4/4, 5/4) via paler brown (M. 7.5 YR 6/4) to very pale brown (M. 10 YR 6/2, 7/2) near edge; colour in KOH 5% distinctly different, greyish brown (M. 10 YR 6/2, 6/3) in basal parts, paler towards edge.

Stem 45–95 × 1.5–5 mm, cylindric, neither rooting nor bulbous, hollow, whitish or sordid white with a slight to very distinct trace of pink, pinkish brown, pale



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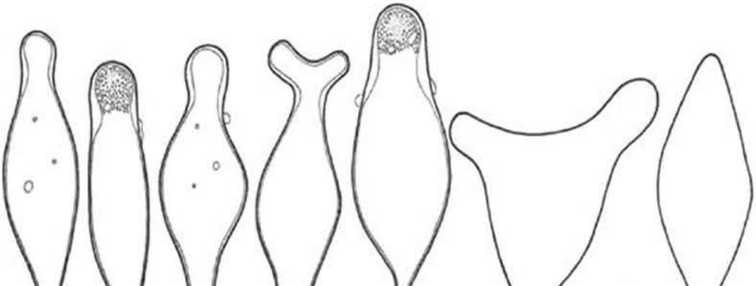

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Figs. 32, 33. *Psathyrella bipellis*. — Pleurocystidiograms (× 575). — 32. 24 July 1966. — 33. 14 Nov. 1970.

purplish pink (M. 2.5 YR 6/2; 5 YR 6/3) or with lilaceous pink flush, particularly in upper half, resulting from purplish pink colour of flesh under purely white and very thin upper layer of tissue, glossy, pruinose at apex, with at extreme base a thin layer of greyish tissue and strigose with white hairs.

Flesh of cap 1.5–3 mm thick, concolorous, dark vinaceous brown to reddish (M. 2.5 YR 2.5/2), particularly in thin layer under surface and over gills; flesh of stem pale purplish pink (M. 2.5 YR 6/4; 5 YR 6/3, 6/4), but with very thin white superficial layer.

Taste and smell not distinctive.

Spore print black.

MICROSCOPIC CHARACTERS.—Spores (11.7–)12.6–15.3(–16.2) × (6.8–)7.2–8.1(–9) μm (averages 13–15 × 7.2–7.6 μm), ellipsoid-amygdaliform, in water dark red, dusky red (M. 10 R 3/2, 3/3, 3/4; 2.5 YR 3/4), in NH_4OH 10% very dark red, dusky red (M. 10 R 3/1, 3/2, 2.5/1, 2.5/2), in KOH 5% very dark to dark greyish brown (M. 10 YR 3/1, 3/2, 3/3), opaque (to subopaque), with apical germ pore 1.5–2 μm wide, normally quite distinct, often even truncate, but in a single collection less distinct and certainly not truncate, in a few to many spores very slightly to distinctly eccentric on the abaxial face, with fairly small hilar appendix.

Basidia 4-, rarely 2-spored, 22–40 × 12.5–15(–16) μm.

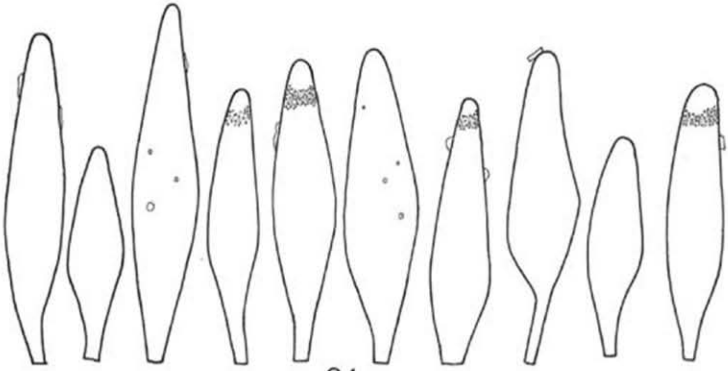
Pleurocystidia abundant, either preponderatingly utriform and subutriform with very obtuse to obtuse apex (forma *barlae*, see observations) or lanceolate fusiform and subfusiform with obtuse to subacute apex (forma *bipellis*, see observations), but in some collections chiefly intermediate forms occur (sublageniform, ellipsoid with very obtuse apex, subcylindric), always with short or somewhat longer stalk, 52.5–95 × 12.5–30 μm, almost always with very slightly thickened (up to 0.5 μm) wall but sometimes many of the utriform and subutriform cells with distinctly thickened wall (up to 1–2 μm) at and particularly just below the apex, practically colourless or very faintly brown in NH_4OH 10%, contents of apical portion of sometimes almost all but more often of only a number or even of very few pleurocystidia with a small to larger amount of amorphous material, very slightly greenish in NH_4OH 10%, including a large to small number of minute droplets (a few of them, however, 1–5 μm in diam.). A few scattered oily droplets often elsewhere in otherwise hyaline pleurocystidia; a few mucoid drops and/or thin elongate or crystal-like deposits, not or scarcely greenish in NH_4OH 10%, often present on outside of walls.

Cheilocystidia 35–75 × 10–25 μm, very densely packed, rendering gill edge sterile, similar to pleurocystidia but shorter and as a result more ventricose, more often with amorphous material (droplets embedded) in their apical portion (sometimes practically in all cells) and more mucoid drops and deposits on their surface, intermixed with a small number of small and scarcely noticeable clavate cells, 10–27.5 × 6–14 μm (sometimes and particularly near margin of cap larger, 15–40 × 10–20 μm, and in somewhat larger numbers), a few of them with a slightly thickened wall and brownish in NH_4OH 10%.

Pigmentation of hymenophoral trama under microscope ('washed' gill mounted in NH_4OH 10%): trama very distinctly coloured from base to edge from brownish membranal pigment; colour strongest at base, fading towards edge; yellowish and thickened hyphal septa and some encrustations present, particularly in basal parts of gill; pigmentation of trama of cap rather strong, with many encrustations.

Cuticle of cap cellular, 2–3 cells deep; its cells, 24–40 μm in diam., hyaline, thin-walled.

Clamps present.



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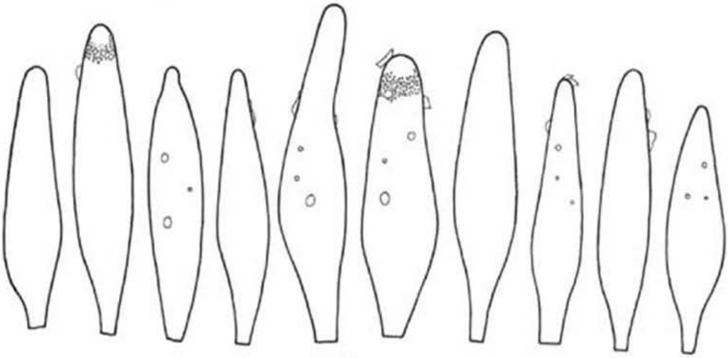

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Figs. 34, 35. *Psathyrella bipellis*. — Pleurocystidiograms (× 575). — 34. 25 Oct. 1974. — 35. 2 Nov. 1974.

HABITAT.—Solitary sometimes gregarious in rich sandy soil of deciduous woods, roadsides in woods.

COLLECTIONS EXAMINED.—NETHERLANDS: prov. Overijsel, Bathmen, castle 'Dorth', 16 June 1974, *J. Daams* (L); prov. Gelderland, Epse, estate ''t Joppe', 16 June 1974, *J. Daams* (L); prov. Noord-Holland, Kortenhoef, 14 Nov. 1970, *J. Daams* (L); Vogelenzang, dunes of Amsterdam Water Supply, 24 July 1966, *E.K.v.W.* (L); Overveen, estate 'Elswout', 25 Oct. 1975 and 2, 5, and 16 Nov. 1976, *E.K.v.W.* (L), Overveen, estate 'Koningshof', 2 Nov. 1974, *C. Bas* (L).

This species is very rare in the Netherlands. In fact our collection of 24 July 1966 was the first recorded in this country, and since then it has only been found in five different places.

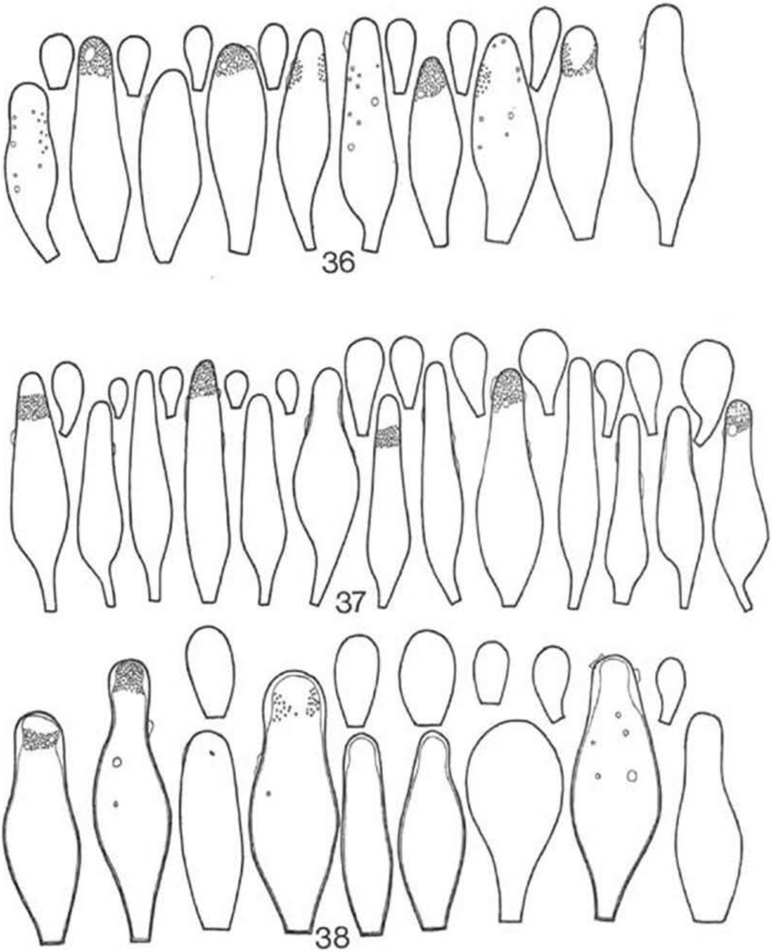
The one specimen (14 Nov. 1970), already in process of drying out, that we received from Mr. Daams was striking in that it was large (cap 40 mm, stem 95 × 4—5 mm) and that the surface of the cap looked exactly like that of specimens of *P. gracilis* f. *corrugis*; all other macroscopical features were, however, typical of *P. bipellis*. Microscopical examination revealed four abnormalities (see Figs. 33, 38, 46): (i) Many spores were small and abnormally shaped, very broadly ellipsoid to almost globose or irregularly shaped, some even more or less triangular with their germ pore sometimes on one side. (ii) The apiculus of all spores was unusually large, hyaline. (iii) A number of pleurocystidia were grossly forked at the apex. (iv) The cell wall of many pleurocystidia was considerably thickened (1—2 μm) in the apical portion. We have regarded this single carpophore as an abnormal manifestation of *P. bipellis*.

Having very carefully examined 25 collections of *P. bipellis* Malençon & Romagnesi (1953: 101) deem it justifiable to distinguish two forms of this species, to which they refer as '*Drosophila bipellis* Quél.' (20 collections, of which 17 from Morocco) and '*Psathyra barlae*' Bres. (5 collections). They give a full description of both forms and come to the conclusion that as for their macroscopical characters, these are practically identical. Romagnesi confirms this conclusion by stating in the 'Flore analytique' (1953: 354) 'Nous ne connaissons actuellement aucun caractère macroscopique bien net pour distinguer les deux formes'. Both are characterized macroscopically by very striking purplish colours of cap, gills, stem, and flesh, and microscopically by very numerous pleurocystidia and further because at least some but usually many of them have an amorphous substance containing many minute oily drops in their apical portion.

To Malençon & Romagnesi it seems that a microscopical and consistent difference between the two forms might exist in that at first the pleuro-cystidia of '*P. barlae*' have a very obtuse apex and no real neck, and later develop into typically utriform cystidia with a wide (7—10 μm) and short neck and capitate apex, whereas those of '*D. bipellis*' are lanceolate subfusiform, their base gradually attenuating towards an obtuse or even subacute apex. They next notice that in Europe and—going by A. H. Smith's publications of 1937 (:219) and 1941 (:39)—also in North America the form with utriform pleurocystidia seems to appear in the spring (May, June), the form with subfusiform cystidia in the late autumn (Oct.-Dec.); this difference also, though not entirely, working out for North Africa.

Checking these observations with Smith's publications of 1937, 1941, and 1972 we found that Smith's descriptions of the pleurocystidia do not sufficiently warrant these conclusions. The collections studied by Smith, for which dates are mentioned, were all found in June and July, whereas the shape of the pleurocystidia mentioned ranges from fusoid, fusoid-ventricose to subutriform.

Malençon & Bertault (1970: 182) while confirming that what they call *Drosophila bipellis* is rare in Europe and more common in North Africa, describe and depict the pleurocystidia as 'lancéolées à subfusiformes, à base renflée et généralement pédiculée, à partie supérieure longuement atténuée en cône à pointe mousse ou subaiguë'



Figs. 36–38. *Psathyrella bipellis*. — Cheilocystidiograms (×575). — 36. Bathmen, 16 June 1974. — 37. 24 July 1966. — 38. 14 Nov. 1970.

and state that the species occurs in November and December but sometimes in spring.

Bresadola (1887: 84) giving summer and autumn for the time of appearance of *Psathyra barlae* in Italy, calls the pleurocystidia 'ampullaceo-stipitate vel subfusiformis', and Horak (1968: 110) who examined Bresadola's type (according to Horak collected in April 1889, this date no doubt being a misprint as the species is described in 1887) found utriform cystidia. Quélet (1884: 501) merely states 'été' for the time of appearance of his *Psathyra bipellis.*

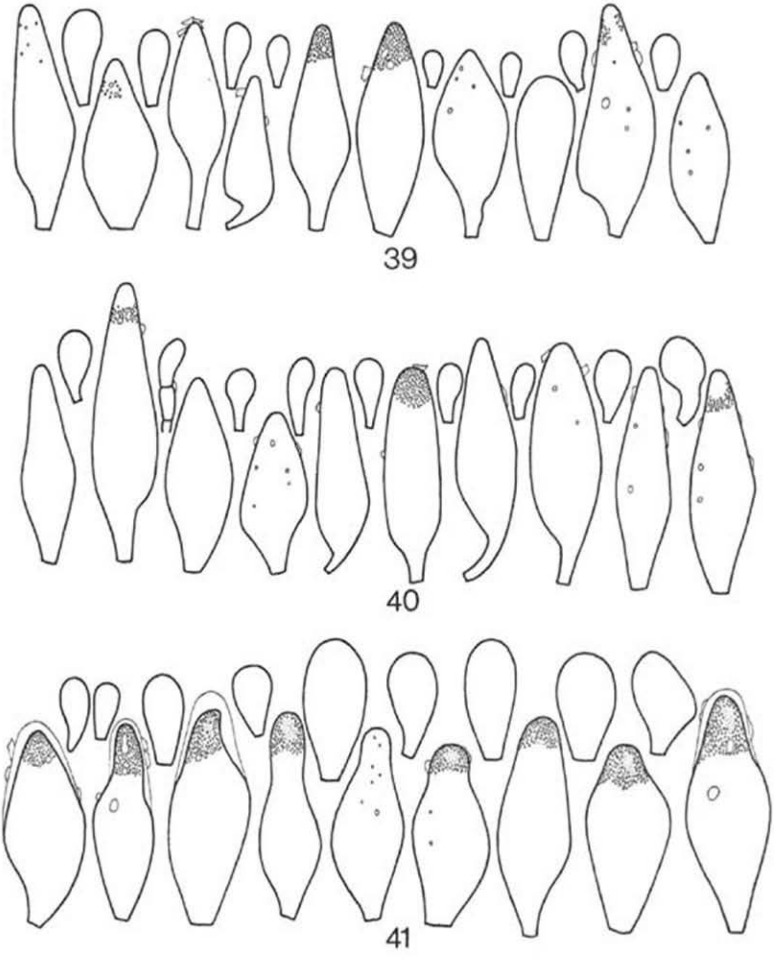
Malençon & Romagnesi (1953: 122—126) make it quite clear both in the text of their paper and by their figures that the shape of the pleurocystidia of '*Drosophila bipellis*' and '*Psathyra Barlae*' varies considerably. The pleurocystidiograms of our own six collections of *Psathyrella bipellis* s.l. also reveal that the shapes of the pleurocystidia vary a great deal and lie in a continuum; they also bear scarcely any relation to the seasonal appearance of the carpophores. The specimens of the mid-summer collection (24 July 1966; Fig. 32) have markedly pedicellate fusoid, by no means utriform pleurocystidia, whereas the in some microscopical respects abnormal specimens of the late autumnal collection (14 November 1970; Fig. 33) have markedly utriform pleurocystidia. The specimens collected on June 16th 1974 (Epse, Fig. 30) had typically utriform pleurocystidia, but those collected on the very same day but elsewhere (Bathmen, not far from Epse) had both utriform, subutriform and fusoid pleurocystidia (Fig. 31). Only the late-autumnal collections (25 Oct. 1974, see Fig. 34; 2 Nov. 1974, see Fig. 35; Nov. 1975, 1976) are in agreement with the observations of Malençon & Romagnesi that late-autumnal specimens seem to have lanceolate, narrowly fusoid pleurocystidia.

In conclusion we feel from both the data in the literature and from our own observations that there is insufficient evidence to warrant the conclusion that a strict correlation exists between the seasonal appearance and the shape of the pleurocystidia of *P. bipellis.* To some extent such a correlation may exist, but in our opinion it cannot serve as an argument to distinguish two species, *P. bipellis* and *P. barlae.* The shape of the pleurocystidia of the specimens on which Quélet based his *P. bipellis*, collected in summer, is unknown.

Although Malençon & Romagnesi (1953: 122—126) do not mention a difference in spore size between the two forms, in their descriptions this size is given as 12—15 × 7—7 × 7.5—8.5 µm for '*Psathyra barlae*' and 12—15—18(—22) × 6—8—9 µm for '*Drosophila bipellis*'. We found the spores of the two collections with distinctly fusiform pleurocystidia also very slightly longer (averages 14.4 × 7.3 µm and 15 × 7.5 µm) than those of the collections with distinctly utriform pleurocystidia (averages 13.4 × 7.5 µm, 13.6 × 7.4 µm and 13 × 7.6 µm) but are not prepared to accept this additional difference between the two 'forms' as sufficient reason to distinguish between them, particularly in view of the limited material studied.

Malençon & Romagnesi describe for '*P. barlae*' the germ pore as fairly small and very slightly eccentric, and for '*D. bipellis*' as large and truncate, without mentioning the position of the germ pore. They do not use this difference, however, in trying to distinguish between the two forms. We found a small to occasionally somewhat larger number of spores with a very slightly eccentric germ pore in five out of our six collections, while the germ pore in the collection from Bathmen (16 June 1974) was very distinct and truncate; the germ pore in the collection from Epse (16 June 1974) was decidedly less distinct and most certainly not truncate; at the same time both collections had markedly utriform pleurocystidia.

According to Malençon & Romagnesi (l.c.) the carpophores with subfusiform pleurocystidia ('*D. bipellis*') might be somewhat larger (cap up to 65 mm, stem up to 130 × 6 mm) than those with utriform pleurocystidia ('*P. barlae*', cap up to 45 mm, stem up to 100 × 6 mm) but obviously there is considerable overlapping (clearly shown by their beautiful colourplate). The colour of the dry cap, Malençon &



Figs. 39–41. *Psathyrella bipellis*. — Cheilocystidiograms (×575). — 39. 25 Oct. 1974. — 40. 2 Nov. 1974. — 41. Epse, 16 June 1974.

Romagnesi think, might be of a slightly different shade (ochre-flesh colour in '*D. bipellis*', sordid greyish-reddish or merely greyish brown in '*P. barlae*') and the gills might turn out to be narrowly adnate in '*D. bipellis*' and broadly adnate in '*P. barlae*' but here again these differences are believed to be slight and dubious, needing —as the authors themselves state—a great deal more verification in the field.

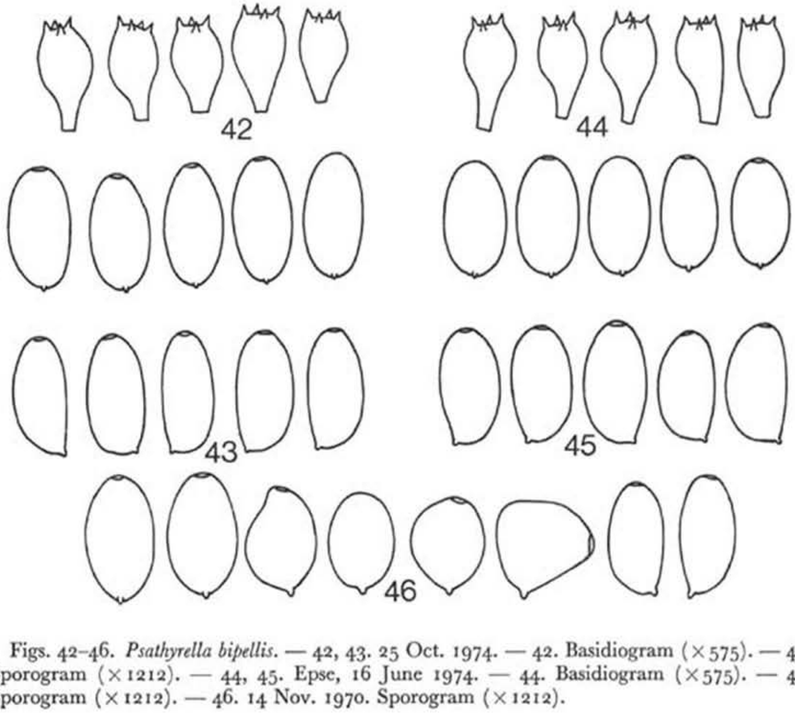
In his earlier paper Smith (1941: 40) thought it questionable whether *Psathyrella barlae* and *P. bipellis* are different species, believing the latter to be a taxon with smaller fruitbodies (cap 10–40 mm) than the former (cap 30–50 mm). Malençon & Romagnesi examined Smith's exsiccata and found both to have utriform and subutriform pleurocystidia. Recently Smith (1972: 104) has come to recognize his former *P. bipellis* as *P. barlae* forma *minor*, of which he examined no less than 21 collections. The difference with *P. barlae* f. *barlae* is said to lie merely in the colour of the young gills (russet-vinaceous in f. *barlae*; bright pink in f. *minor*), the 'clearly terrestrial habitat' (but for f. *barlae* the habitat is given as 'on soil and humus') and the small size; it is particularly stated that the two forms are similar in pigmentation as observed on dried material and mounted in KOH as well as in spore features and cystidia. In our own material the diameters of the caps varied from 18 to 40 mm, the lengths of the stems from 25 to 95 mm.

POSITION OF P. BIPELLIS IN THE GENUS PSATHYRELLA.—*Psathyrella bipellis*, because of its large spores and short, thickset basidia, obviously belongs to subgenus *Psathyrella*. Because of its habit, size, purplish colours, numerous pleurocystidia of which at least some but usually many contain an amorphous substance and oily droplets in their apical portion, the species cannot be ranked with those of section *Atomatae*. Above all because of its non-rooting stem and further because of its purplish colours and its pleurocystidia the species cannot be ranked with those of section *Psathyrella* either. It therefore merits the separate section already erected by Malençon & Romagnesi (1953: 117).

Smith (1972: 103) places the species under the name *P. barlae* in *Psathyrella* subgenus *Pannucia* section *Appendiculata*, a characteristic of this section being that the margin of the cap is appendiculate from remains of a submembranous to membranous inner veil. But neither in our collections nor in those described by Malençon & Romagnesi (l.c.) and Malençon & Bertault (1972: 182) was a truly appendiculate veil observed. The same applies to the fruitbodies depicted on Smith's plates 75a and b (1972) while Smith himself in his description of *P. barlae* does not describe the veil as appendiculate. It therefore looks as if in Smith's classification *P. bipellis* should be placed in section *Pannucia* of subgenus *Pannucia* rather than in section *Appendiculata*.

As Smith himself considers the veil features in this species rather variable and inconspicuous, the species has also been keyed out by him in subgenus *Psathyrella*. Because of its large spores and utriform pleurocystidia we find it here in section *Umbonata*, where it adjoins the very closely related *P. pseudocorrugata*, a new species, based on one collection. As for the macroscopic and microscopic characters this species is said to be fully identical with *P. barlae*, differing only from that species by the pileus trama staining vinaceous brown in KOH. But although Smith places his *P. pseudocorrugata* in subgenus *Psathyrella* section *Umbonatae*, which is characterized by utriform pleurocystidia, it is clear from his description and particularly his figures that its pleurocystidia are not utriform but 'elliptic pedicellate to ovate-pedicellate to fusoid-ventricose' as Smith correctly calls them. This would constitute a second difference with *P. barlae* the pleurocystidia of which Smith depicts and describes correctly as 'subutriform to fusoid-ventricose, sometimes subcylindric'. The shape of the pleurocystidia in *P. pseudocorrugata* would make that species identical with Malençon & Romagnesi's '*Drosophila bipellis*' except for the pileus trama staining vinaceous brown in KOH.

We checked the colour of 'washed' sections of the caps of dried material, deprived of their gills and mounted in KOH 5%. In both our specimens with utriform and fusoid pleurocystidia we found it to be sordid greyish brown (M. 10 YR 5/2, 5/3) under the binocular lens, and sordid brown (M. 10 YR 5/3, 5/4) under the microscope, a vinaceous tinge being totally absent. This then rules out *P. pseudocorrugata* for



Figs. 42–46. *Psathyrella bipellis*. — 42, 43. 25 Oct. 1974. — 42. Basidiogram (× 575). — 43. Sporogram (× 1212). — 44, 45. Epse, 16 June 1974. — 44. Basidiogram (× 575). — 45. Sporogram (× 1212). — 46. 14 Nov. 1970. Sporogram (× 1212).

any of our specimens but in view of the great variability of *P. bipellis* we feel that the validity of *P. pseudocorrugata* needs confirmation.

In his observations on *P. barlae*, Smith (1972: 104) states that the fusoid pleurocystidia of *P. bipellis* as described by Malençon & Romagnesi would place that species in a different section, though not stating in which. We assume Smith meant section *Psathyrella* (pleurocystidia acute to obtuse) and within this, because of the large spores, subsection *Psathyrellae* and further, because of the absence of pink tints on pileus margin or gill edges particularly of faded basidiocarps, in series *Tenerae*. In that series *P. barlae* is indeed mentioned, this time in connection with another new species, *P. subincarnata*. *Psathyrella subincarnata*, however, is said to have no veil and narrowly fusoid-ventricose pleurocystidia with elongated neck; the three cystidia of this species depicted in Fig. 662 indeed do not resemble those of *P. bipellis* at all.

NOMENCLATURE.—Because of its very striking macroscopic features, particularly its beautiful purple colours, any mycologist who knows about *P. bipellis* but has never seen it, should be able to recognize this rare species at first sight when he comes across it in the field. We can therefore safely rely on the description and pictures given by Quélet (1884: 501) pertaining to the species described above as well as by Malençon & Romagnesi (1953: 122–126) although Quélet does not give microscopic details and although his pictures are rather schematized and show a violet instead of a purple colour of the cap. For reasons given above *P. barlae* as described and depicted by Bresadola (1887: 84) should be considered as a form of *P. bipellis*, having utriform pleurocystidia. Bresadola's plate represents the species better than Quélet's.

In their thorough treatise 'Le complexe "*Psathyra corrugis*"' Malençon & Romagnesi (1953: 101) give a very comprehensive survey of the synonymy of *P. bipellis*. They place *Psathyra corrugis* (Pers.) Quél. ss. Ricken first in the list of likely synonyms and take great pains in critically reviewing the literature on that species in an attempt to reveal the true identity of *A. corrugis* as described by both Persoon (1794: 24; 1801: 424) and Fries (1821: 298). In the end they conclude that the epithet '*corrugis*' was a nomen confusum and should be rejected. They could have saved themselves this extensive study of the literature by examining the material of *Agaricus corrugis* in Persoon's herbarium at Leiden (L. 910.258–411) as Singer (1961: 18) and we (1971a: 261) did. Examination of that material clearly showed that *A. corrugis* is a species quite different from *P. bipellis*, being merely a form of *P. gracilis*.

It is now generally accepted that *Psathyra corrugis* ss. Ricken stands for both forms of *Psathyrella bipellis*. Ricken's description and plate 67 fig. 3 are in full agreement with the species described above and by Malençon & Romagnesi. The latter authors draw attention to the fact that Ricken collected his *Psathyra corrugis* from May till November and describes the pleurocystidia as ventricose-fusoid, 10–12 μm wide and often with swollen apices. From this they conclude that Ricken's description covers both '*Drosophila bipellis*' and '*Psathyra barlae*'.

Agaricus (*Hypholoma*) *canofaciens* Cooke, described by Cooke in Grevillea (1885: 1) and depicted later (1884–1886: plate 595/621) is likely to be synonymous with *P.*

bipellis, as was suggested by Malençon when he and Romagnesi started their research on *P. bipellis*. They finally reject Cooke's name as a synonym chiefly because of the very dark brown colour of both cap and stem (the latter particularly very dark at its base, according both to the description and Cooke's plate), according to Malençon & Romagnesi not showing any trace of purple or a vinaceous hue. But in the description the cap is called dark bay brown (=reddish brown, chestnut brown), the flesh of the stem rufescent. In comparing the colours of Cooke's plate with the Munsell charts we found the cap to be indeed dark reddish brown, but we agree with Malençon & Romagnesi that particularly the colour of the stem (dark brown, M. 7.5 YR 4/2) does not fit in at all with *P. bipellis*. Cooke calls the flesh of the stem rufescent, gradually darker downwards, which is not a feature of *P. bipellis* either. The spore size, given by Cooke as very large (12—7×8 μm) and the size and stature of the carpophores correspond very well with *P. bipellis*. As the very dark stem of *P. canofaciens* makes the synonymy a bit doubtful we have included the name in the list of synonyms with a question mark.

Agaricus (*Psilocybe*) *atro-rufus* Schaeff. ss. Cooke as depicted by Cooke (1884–1886 pl. 571/602) and later described by him (1887: 211) corresponds very well with *P. bipellis* as to colours, size and habit and may because of this be added to the list of synonyms of *P. bipellis*, be it also with a question mark, as we have not seen authentic material.

Judging by the description given by Saccardo (1899: 154) of *Psathyra roseolo* (Clem.) Sacc., originally described by Clements (1896: 23) as *Gymnochilus roseolus* and mentioned by Smith (1941: 40) as somewhat intermediate between *P. barlae* and *P. bipellis*, is almost certainly synonymous with *P. bipellis*. Not having seen authentic material Smith hesitated to dispose of it either way. We have included the name in the list of synonyms with a question mark for the same reason.

Although some authors (Konrad & Maublanc 1924: 80; Rea 1922: 418; Ricken 1913: 257) believe that *Agaricus helobius* as described and depicted by Kalchbrenner (1874: 31, pl. 17 fig. 4) might be conspecific with *P. bipellis*, we follow Malençon & Romagnesi (1953: 101) who clearly reason that Kalchbrenner's description of *Agaricus helobius* cannot pertain to *P. bipellis*, bringing forward arguments with which we fully agree and for which we refer to their paper.

PSATHYRELLA section SUBATRATAE (Romagn.) ex Sing.

Drosophila sect. *Subatratae* Romagn. *in* Bull. mens. Soc. linn. Lyon **13**: 53. 1944. (not val. publ.; no Latin descr.). — *Psathyrella* sect. *Subatratae* (Romagn.) ex Sing. *in* Sydowia **15**: 68. 1961. — Type: *Psathyrella subatrata* (Batsch ex Fr.) Quél.

Romagnesi (1944: 53) with a description in French founded the section *Subatratae* for what he then called *Drosophila subatrata* (Batsch ex Fr.) Quél. ss. Ricken, this species obviously being *P. conopilus* as described below. In his short description he stresses the absence of pleurocystidia and of a veil ('voile rigoureusement nul'; the word 'nul' even in italics), and the spores are called large, 12–16 μm. Singer (1961: 68), validating Romagnesi's sectional name, states 'velo nullo', accepting *P. subatrata* (Batsch ex Fr.) Quél. as type species. Earlier (1951: 469) Singer had already written about section *Subatratae* 'veil absolutely none, allegedly even in the primordia (at least macroscopically)' and he repeats this statement later (1962: 511). Section *Subatratae* (Romagn.) ex Sing. *emend.* A. H. Smith (1972: 271) differs from section *Subatratae* as originally described by both Romagnesi and Singer in that in four out of its 26 species remnants of a veil were said to be observed, while in only a few is the absence of a veil specifically mentioned. Moreover, the 17 species of series *Atricastanae* of Smith's section *Subatratae* have small spores (5–10 μm long).

PSATHYRELLA CONOPILUS (Fr.) Pearson & Dennis—Figs. 4–12, 47–52

Agaricus conopilus[1] Fr., Syst. mycol. **1**: 504. 1821. — *Psathyra conopilus* (Fr.) Kummer, Führ. Pilzk.: 70. 1871. — *Drosophila conopilus* (Fr.) Quél., Enchir.: 116. 1886. — *Coprinarius conopilus* (Fr.) Schroeter *in* F. Cohn, kryptogFl. Schles. **3** (1): 564. 1889. — *Pratella conopilus* (Fr.) Coutinho, Eubasid. Lusit. Herb. Univ. Olisip.: 92. 1919. — *Psathyrella conopilus* (Fr.) Pearson & Dennis *in* Trans. Brit. mycol. Soc. **31**: 185. 1948. — *Drosophila subatrata* var. *conopilus* (Fr.) Kühn. & Romagn., Fl. anal.: 354. 1953.

Agaricus subatratus Batsch, Elench. Fung. **2**: 103. 1786; *ex* Fr., Epicr.: 238. 1838. — *Psathyrella subatrata* (Batsch ex Fr.) Gill., Champ. France Hym.: 616. 1878. — *Psathyra subatrata* (Batsch ex Fr.) Quél. *in* Bull. Soc. Amis Sci. Rouen II **15**: 161. '1879' [1880]. — *Drosophila subatrata* (Batsch ex Fr.) Quél., Enchir.: 117. 1886. — *Coprinarius subatratus* (Batsch ex Fr.) Coutinho, Eubasid. Lusit. Herb. Univ. Olisip.: 87. 1919. — *Psathyra conopilus* var. *subatrata* (Batsch ex Fr.) J. E. Lange *in* Dansk bot. Ark. **9** (1): 14. 1936.

Agaricus superbus Jungh. in Linnaea **5** (1): 388. 1830. — *Psathyra conopilus* Fr. var. *superbus* (Jungh.) Cke., Ill. Brit. Fungi: pl. 1158/1185. 1889–1891.

Agaricus arata Berk., Outl. Brit. Fungology: 176. 1860. — *Coprinus aratus* (Berk.) Berk. & Br. ('Notices Brit. Fungi') *in* Ann. Mag. Nat. Hist. V **9**: 181. 1882. — *Psathyrella arata* (Berk.) W. G. Smith, Syn. Brit. Basidiom.: 200. 1908.

Psathyra elata Massee, Brit. Fungus Fl. **1**: 353. 1892.

? *Agaricus graciloides* Schulz. *in* Verhandl. Kaiserl.-Königl. zoöl.-bot. Ges. Wien **26**: 415. 1877.

Agaricus graciloides Peck *non* Schulz. *in* Rep. N.Y. State Mus. **30**: 42. 1878. — *Psathyrella graciloides* (Peck) Sacc., Syll. Fung. **5**: 1127. 1887.

Psilocybe castaneicolor Murrill *in* Mycologia **15**: 19. 1923.

SELECTED DESCRIPTIONS.—Ricken, Blätterp.: 262, 264. 1913 (as *P. subatrata*); J. E. Lange, Fl. agar. dan. **4**: 99, 100. 1939 (as *P. conopilus* var. *subatrata*); Kühn. & Romagn., Fl. anal.: 354. 1953 (as *Drosophila subatrata*); Malençon & Bertault, Fl. Champ. sup. Maroc **1**: 195. 1970 (as *Drosophila subatrata*); A. H. Smith, North American species of *Psathyrella in* Mem. N.Y. bot. Gdn. **24**: 273. 1972.

SELECTED ILLUSTRATIONS.—Fries, Icon. select. Hymen. **2**: 38, pl. 139 fig. 1; Gillet, Tabl. anal. Hymen.: pl. 582, 590. 1884 (as *P. subatrata*); Cooke, Ill. Brit. Fungi **5**: pl. 575/609.

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[1] As has been pointed out by Singer (1975: 504), the epithet was written '*conopilus*' by Fries in 1821, and should not change with the gender of the generic name with which it is combined.

1884–1886; **5**: pl. 633/634. 1886–1888 (as *A. subatratus*); **5**: pl. 636/637. 1886–1888 (as *A. aratus*); **8**: pl. 1158/1185. 1889–1891 (as *A. conopilus* var. *superbus*); Ricken, Blätterp.: pl. 68, fig. 3. 1913 (as *P. subatratus*); J. E. Lange, Fl. agar. dan. **4**: pl. 155 D, pl. 155 E. 1939 (as *P. conopilus* var. *subatrata*).

Chief characteristics.—Solitary to gregarious; cap 25–55(–65) mm (in small form 10–25 mm), conical, dark reddish brown, very soon dark brown, hygrophanous, alutaceous without pink when dry, often rugulose, rarely rugose; veil none; gills moderately broadly to narrowly adnate, tobacco colour or dark purplish brown, with white edge; stem 90–190 × 2–3 (apex) × 2.5–5 (base) mm (in small form 45–75 × 2–3.5 mm), not rooting; spores 13.5–17 × 6.5–8 μm, with eccentric germ pore; pleurocystidia absent; cheilocystidia densely packed, shape and size very variable, varying from large lageniform with long neck, 40–70 × 10–20 μm, with neck 5–10 μm wide, to small ventricose subutriform, 30–50 × 15–20 μm; spheropedunculate cells present in varying quantities; hymenophoral trama distinctly coloured; cuticle of cap a palissade of globose to clavate cells; dark yellow-brown, hollow, thick-walled, 100–400 μm long, setae springing from hypodermis.

Macroscopic characters.—Cap in very young stages ellipsoid, 3–4 mm in diam., 5–6 mm high, with margin appressed to stem, not striate, dark reddish brown (M. 5 YR 2/4; 5 YR 3/3, 3/4); when slightly older and larger conical and soon striate, in maturity 25–55(–65) mm in diam., 20–35 mm high (in small form 10–25 mm in diam. and 8–15 mm high), conspicuously conical, at most paraboloid-conical, in final stages only slightly spreading, conspicuously dark reddish brown (M. 5 YR 3/3, 3/4, 4/4) when still very fresh but usually when found already lacking this red hue and merely strikingly dark brown (M. 7.5 YR 4/4), finely striate up to half-way or 2/3 from margin upwards, sometimes almost to centre, hygrophanous, process of drying setting in quickly and starting at apex, colour changing either via yellowish brown (M. 7.5 YR 5/6, 6/6) or dark sordid brown (M. 10 YR 3/2, 3/3, 4/4) to finally alutaceous, very pale yellowish brown or greyish (M. 10 YR 6/4, 7/3, 7/2, 8/4, 8/3) at centre slightly darker (M. 10 YR 7/4), without pink shades, sometimes slightly micaceous, often slightly rugulose, rarely strongly rugose, with smooth and matt surface.

Veil none.

Gills 4–6 mm broad (in small form 3–4 mm), ventricose only near margin of cap, then straight (rarely slightly ventricose) and strongly ascending, moderately broadly to rather narrowly adnate without tooth, crowded, their face in very young specimens pale brownish grey (M. 10 YR 6/2, 6/3) near edge, the remainder distinctly brown (M. 7.5 YR 5/2, 5/6, 6/6), in mature specimens tobacco colour or purplish brown (M. 5 YR 2/2, 3/2; 7.5 YR 3/2, 4/2; 10 YR 3/2, 3/3), near edge sometimes somewhat greyer (M. 10 YR 5/2, 4/2) with white and minutely fimbriate edge. Trama of 'washed' gill under binocular lens hyaline, distinctly pale brown, darkest (M. 10 YR 6/4, 6/3) in basal part and sometimes up to half-way edge, paler (M. 10 YR 7/4, 7/3, 7/2) towards edge, and near and at edge very pale brown or grey (M. 10 YR 8/3, 7/2, 7/1) to practically colourless.

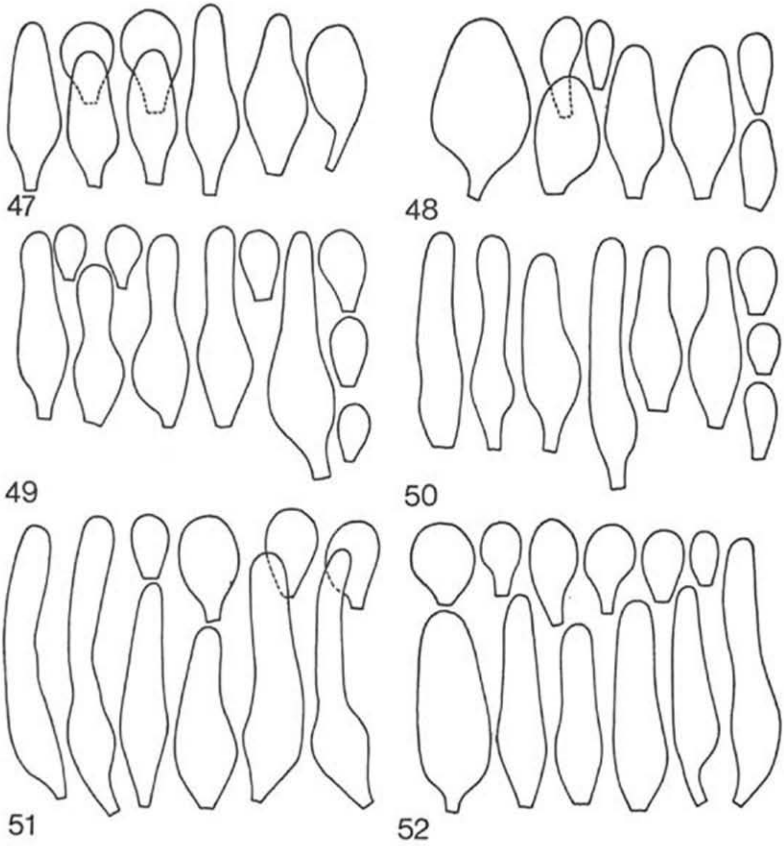
Stem 90–190 × 2–3 mm (apex) to 2.5–5 (base) mm (in small form 45–75 × 2–3.5 mm) with extreme base sometimes slightly clavate or even subbulbous, 4–7 mm in diam., and strigose with white hairs, not rooting, white or whitish and often pale isabelline or pale brown lower down, smooth and glossy, hollow, with pruinose and sometimes finely striate apex, in very young stages longitudinally fibrillose.

Flesh of cap 1–2.5 mm thick in centre, in young or very fresh caps dark reddish brown (M. 2.5 YR 2/4; 5 YR 3/3, 3/4), very soon via greyish brown (M. 10 YR 4/2, 4/3) to sordid white; flesh of stem pale brown (darkest at base), with thin superficial white layer.

Smell and taste not distinct.

Spore print black.

MICROSCOPIC CHARACTERS.—Spores (12.6–)13.5–17.1(–18) × 6.3–8.1(–9) µm (averages 13.7–15.8 × 7.2–7.9 µm), smooth, ellipsoid-amygdaliform, in water dark reddish brown (M. 10 R 3/3, 3/4; 2.5 YR 3/4, 2.5/4), in NH_4OH 10% scarcely darker and browner (M. 10 R 2.5/2, 3/3; 2.5 YR 3/2, 2.5/4), in KOH 5% very dark greyish brown (M. 10 YR 3/2), subopaque (but some opaque, particularly when spores are mounted in NH_4OH 10%); with fairly small hilar appendix; with apical germ pore varying from one collection to another and even between spores of one gill from very



Figs. 47–52. *Psathyrella conopilus.* — Cheilocystidiograms (× 575). — 47. 7 Oct. 1961. — 48. 8 Nov. 1962. — 49. 23 Oct. 1965. — 50. 8 Oct. 1966. — 51. 15 Nov. 1968. — 52. 3 Oct. 1975.

to less distinct and from very slightly to quite distinctly eccentric, 2–2.5 μm wide, normally not but sometimes distinctly be it slightly truncate; apex of spore normally rounded but in spores with distinctly eccentric germ pore occasionally oblique and straight at site of germ pore.

Basidia (20–)22–40(–42) × 11–15(–16) μm, 4-spored.

Pleurocystidia absent.

Cheilocystidia very numerous, versiform and normally densely packed; on the whole either preponderatingly if not almost exclusively lageniform with long or fairly long or short, thin or thick, cylindrical or subcylindrical neck either sharply delimited from or gradually broadening towards ventricose cell body, 40–77 × 10–20 (—27) μm with 5–10 μm wide neck; or preponderatingly if not almost exclusively small, ventricose, subutriform or sometimes even utriform, subfusiform, 30–47(–55) × 15–20 μm, with both forms normally occurring intermixed, their mutual proportions varying a great deal from one collection to another, from one specimen to another in the same collection, and from one gill to another in the same specimen, intermediate forms frequently occurring. At their base with scarcely any to a fair number (30–70% of total number of marginal cells) of spheropedunculate cells (often difficult to find) either preponderatingly small (10–25 × 7.5–15 μm) and subglobose to clavate, or larger (15–30 × 12.5–22.5 μm) and globose to subglobose (particularly when cheilocystidia less crowded). All these cells more or less thin-walled, colourless and without mucus or crystals, but cheilocystidia often having very slightly thickened walls.

Pigmentation of hymenophoral trama under microscope ('washed' gill mounted in NH_4OH 10%): trama distinctly coloured from membranal pigment, yellowish brown in basal half and strongest at base to yellow towards and at edge, with a large number of thickened yellow hyphal septa in basal half, particularly at base, with few encrustations.

Cuticle of cap formed by a palissade of closely packed cells, chiefly globose or subglobose, some clavate, hyaline, colourless but often a few with slight brown tinge, with very short to somewhat longer stalk, the latter often with slightly thickened and yellowish brown (in NH_4OH 10%) wall and a few encrustations; fairly numerous, scattered, thick-walled, dark yellowish brown, 100–400 μm long setae very gradually tapering from the swollen base (6.4–9.6 μm) to the apex (2.5–3.2 μm), springing from the hypodermis.

Clamps present at hyphae of stem and cells of subhymenium.

HABITAT.—Solitary to often gregarious (not cespitose) in rich soil or humus, in deciduous woods, on rubbish heaps, on decaying material and always against small pieces of wood or dead branches. July-November, fairly common.

COLLECTIONS EXAMINED.—NETHERLANDS: prov. Overijsel, Deventer, estate 'Colmschate', 8 Oct. 1966, *E.K.v.W.* (L); prov. Utrecht, Amerongen, 16 Oct. 1960, *C. Bas* (L); Zeist, estate 'Nienhof', 22 Sept. 1962, *A. F. M. Reijnders* (L); Bunnik, estate 'Oud-Amelisweerd', 22 July 1954, *R. A. Maas Geesteranus* (L); Nieuwersluis, estate 'Over-Holland', 8 Nov. 1962 and 13 July 1968, *E.K.v.W.* (L); prov. Noord-Holland, Vogelenzang, dunes of Amsterdam Water Supply, 7 Oct. 1961, *E.K.v.W.* (L); Vogelenzang, estate 'Leyduin', 22 Sept. 1964, *E.K.v.W.* (L); Overveen, estate 'Elswout', 23 Oct. 1965, 25 Oct. 1974, 3 Oct. 1975, and 29 Oct. 1976, *E.K.v.W.* (L); Castricum, dunes of Province North-Holland Water Supply, 11 Nov. 1967 and 30 Sept. 1975, *E.K.v.W.* (L); prov. Zuid-Holland, Wassenaar, estate 'Zuidwyk', 30 Oct. 1954, *C. Bas* (L); Oostvoorne, estate Mildenburg, 7 Oct. 1956, *R. A. Maas Geesteranus* (L); Goedereede, Oostdijkscheweg, farm 'Zeezicht', 15 Nov. 1968, *E.K.v.W.* (L); prov. Limburg, Maastricht, St. Pietersberg, 19 Oct. 1950, *R. A. Maas Geesteranus* (L); Maastricht, Cannerbosch, 10 Nov. 1951, *R. A. Maas Geesteranus* (L).

Fries (1874: 313) already states that apart from the far and away most common, tall form of *P. conopilus* (stem 100–125 mm long) a medium sized form occurs (stem 50–75 mm long), and even a small form (stem 25 mm long). This observation is confirmed by a few authors: Bel (1889: 122) mentions 40–120 mm for the length of the stem; Stevenson (1886: 343) in distinguishing a large, an intermediate and a small form of *A. subatratus* and giving the same figures as Fries probably copied these from Fries; with Wakefield & Dennis (1950: 20) the length of the stem goes up to only 60 mm; with Rea (1922: 419) the length varies from 25 to 125 mm. Large gregarious groups of specimens usually comprise a few smaller specimens, but occasionally all specimens of a collection are small, and this may well impede recognition in the field. Three out of our own 18 collections (8 Nov. 1962, 11 Nov. 1967, 13 July 1968) consisted exclusively of medium-sized carpophores (stems 60, 45–75 and 30–50 mm long). We feel it is not warranted, however, to formally distinguish a small form of *P. conopilus*.

The process of drying sets in so quickly that one normally finds the caps to be merely dark brown (M. 7.5 YR 4/4), all traces of red having already disappeared; the specimens nevertheless still look quite fresh. One often finds all or almost all the caps of a collection already dry and alutaceous. In the past this has led to erroneous descriptions and misinterpretations of the species.

The cause of the very smooth and matt appearance of the dry caps of *P. conopilus*, resembling the surface of dry caps of species of the genus *Conocybe*, is probably that the cuticle of the cap consists of a palissade of spheropedunculate cells instead of the usually 2–4 cells deep layer of globose to subglobose cells. The former very much resemble those of the cuticle of species of *Conocybe*, be it that the stalks are shorter.

As for the cystidia, Romagnesi (1953: 354) states in bold face letters that they occur exclusively on the edge of the gills; adding between brackets, however, the word 'presque'. With our technique of carefully removing the gill edge from the gill and then studying both the edge and the remaining part of the gill under separate coverslips under the microscope we have never come across pleurocystidia in *P. conopilus*. Smith (1972: 273) also reports the absence of pleurocystidia in *P. conopilus*. In his definition of the section *Subatratae*, Romagnesi (1944: 53) truly describes the cystidia as being variable; he also calls them subutriform. As stated in our description and depicted in our figures they are very often lageniform, while many intermediate forms (subfusiform, sublageniform, subcylindrical) frequently occur.

All authors agree on the absence of a veil in *P. conopilus*, and most authors describe the stem as having a pruinose apex. Smith (1972: 273), however, calls the veil 'rudimentary or lacking' and does not mention the stem as being pruinose at the apex. Smith also states—and this tallies with the latter observation—that he has not found caulocystidia on revived material. We cannot endorse these observations. In our own material we have never come across remnants of a veil on either cap or stem; we always found the apex of the stem to be distinctly, though not strongly and often only slightly, pruinose, in accordance with the latter observation we found caulocystidia in abundance on the apex of the stem. The caulocystidia are identical with the cheilocystidia and of either the same size or slightly larger.

Psathyrella conopilus is first mentioned by Fries in Syst. mycol. (1821: 504) where he compares his *Agaricus conopilus* with *A. conocephalus* Bull., from which species he considers it to differ. With Ricken (1913: 69) the latter species is *Bolbitius conocephalus* (Bull.), a species supposed to belong to the genus *Galerella* by Singer (1975: 518).

Although the description of 1821 is very brief and far from clear, indicating only a few characters, it can be taken as the first formal description of our *Psathyrella conopilus*. In Epicrisis (1838: 238) Fries gives his first description of *A. subatratus*, together with a description of *A. conopilus*. In all his works Fries places *P. conopilus* in tribus *Psathyra*, *P. subatrata* in tribus *Psathyrella*; one wonders why. In Monographia Fries (1857: 438) stresses the great analogy between the species of *Psathyra* and those of *Psathyrella*, the former to be distinguished from the latter because their spores are dark brown and not black and their gills are dark brown or purplish. In the same work Fries (1857: 438) states about *A. conopilus* that the gills become 'cum sporis fusco-purpurascentes' (colour of the spore print unfortunately not mentioned separately) and about *A. subatratus* (1863: 305) that the gills are 'fuligineo-nigricantes, fere umbrinae' (therefore also some shade of brown) and the spore print black. In the Icones (1877–1884, pl. 139, fig. 1) the gills of *A. subatratus* are depicted as very distinctly brown, tobacco brown. The caps of *A. conopilus* are called 'ex albido pallescens', no striation being mentioned, whereas the caps of *A. subatratus* are called 'pulchre rufescenti-umbrinus, siccus rufescenti-pallidus' and 'circa marginem striatulus'. The description of all other characters (sizes of cap and stem, habit, attachment and crowding of gills, smoothness and rigidity of stem, etc.) is the same or nearly so. From these descriptions and also from those in Epicrisis, Hymen. europ. and the Icones, the conclusion is justifiable that *A. conopilus* cannot but represent the dry stage of *A. subatratus*.

Although quite a number of authors (Gillet, 1878: 582, 616; Ricken, 1913: 262, 264; Lindau, 1917: 126; Rea, 1922: 413, 419; Bigeard & Guillemin, 1913: 99, 100; Buch, 1952: 273, 274; Lange, 1939: 99, 100; Moser, 1967: 213, and others) give separate descriptions of both *P. conopilus* and *P. subatrata*, it is sufficiently clear that *P. conopilus* as interpreted by these authors pertains to the dry form of *P. subatrata*. Plate 155 D (*Psathyra conopilus*) and plate 155 E (*Psathyra conopilus* var. *subatrata*) given by J. E. Lange (1939) illustrate this best.

Romagnesi (1953: 354) calls the species *Drosophila subatrata* with a var. *conopilus*, of which the caps are higher, have a more acute apex and are remarkably rugose in the dry stage, whereas the spores are said to be very slightly smaller.

Malençon & Bertault (1970: 195), following Romagnesi's nomenclature, add yet another difference in that the carpophores of var. *conopilus* ss. Romagn. are supposed to be larger. From our own material we have been unable to lend support to the statements by either Romagnesi or Malençon & Bertault. The caps of almost all our collections were to some extent rugulose in the dry stage, and the only collection (plm. 20 specimens, 13 July 1968) in which dry caps were conspicuously rugose consisted of medium sized carpophores (stems 45–75 mm long) of which the spores were not smaller than those in the other collections (average 14.7 × 7.3 μm) and the caps not outstandingly conical.

Singer (1975: 504) quite recently mentions the two supposed taxa as separate species. Dennis, Orton & Hora (1960: 144) are the first to realize and proclaim the conspecifity of *P. conopilus* and *P. subatrata*; A. H. Smith (1972: 273) followed suit.

Judging by the descriptions given by Berkeley (1860: 176) of *A. aratus*, later by Berkeley & Broome (1882: 181) of *Coprinus aratus* (Berk.) Berk. & Br. and again later by W. G. Smith (1908: 200) of *Psathyrella arata* (Berk.) W. G. Smith, this species must be conspecific with *P. conopilus*. Indeed, Pearson & Dennis (1948: 185) state that Cooke's plate 636/637, depicting *A. aratus*, though unusually sulcate as they put it is hardly distinct from *P. conopilus*. Both the latter authors and Dennis, Orton & Hora (1960: 144) also state that Massee's *P. elata* (1892: 353) is conspecific with *P. conopilus*.

A. H. Smith (1972: 274) examined the type material of *Psilocybe castaneicolor* Murrill (1923: 19) and *A. graciloides* Peck (1878: 42) and found these specimens identical with *P. conopilus*. Schulzer von Müggenburg (1877: 415) also names a species *Agaricus graciloides*, doing this just one year before Peck describes his species. Going by Schulzer's description his species very probably also represents *P. conopilus*, but as we did not examine type material we have given the name with a question mark in the synonymy.

Under *A. conopilus*, Fries (1838: 231 and 1874: 304) already referred to the description and picture Junghuhn (1830: 388, pl. 6 fig. 11) had given of his *A. superbus*, a species clearly representing *P. conopilus*.

The description Benoist (1899: 163) gives of his *Psathyrella circellatipes* corresponds in every way with medium sized specimens of *P. conopilus*, except that he reports that in very young specimens the entire cap and stem are covered with reddish orange hairs, that later both cap and stem become smooth, the stems then being covered with white hairs only at the extreme base, above which one or several about 1 mm broad, torn, reddish orange annular zones occur, rarely replaced by a fibrous zone of the same colour. From this description it seems that both the hairs and the annular zones are remnants of an ozonium, the more so as Benoist adds that the colour is the same as that of the membranous mycelial remnants, often adhering to the base of the stems. Benoist's specimens, moreover, did not grow solitary but cespitose against oak wood.

Malençon & Bertault (1970: 196) mention the occasional presence of 'méchules fauve vif par les débris d'un Ozonium' at the base of the stem. Such fibrils were noticed only in one of our collections (30 Oct. 1954) and were described by the collector as delicate loose fibrils which were pale ochre brown only in the largest specimen of the collection.

Benoist's species is mentioned only by Bigeard & Guillemin (1913: 300), who merely copy Benoist's description. Romagnesi (1953: 354) regards Benoist's species as merely a form of *Drosophila subatrata*, and Smith (1972: 274) regards the species as one in its own right and even describes a small-spored variety of it, viz. var. *microspora*. With Smith the stem has brownish flecks of tomentum near the base with some tawny mycelium around the base in young basidiocarps, which Smith also calls ozonium. In all other respects Smith's description tallies with the medium sized forms of *P. conopilus* (stems 40—70 × 1.5—4 mm), except that he calls the gills ventricose (his plate 74, however, shows rather straight to only slightly ventricose gills), that here he did find caulocystidia, and above all that the growth is cespitose (as clearly depicted on his plate 74). Smith does not report the actual presence of coloured annular zones as described by Benoist. We feel that the relatively small size combined with the cespitose growth, and not the remnants of the ozonium would lend support to regarding this species, which we have never come across, as a variety of *P. conopilus*.

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A NEW BLUING SPECIES OF PSILOCYBE FROM EUROPE

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(With 10 Text-figures)

A probably hallucinogenic new species, *Psilocybe liniformans*, is described. It is compared with *P. fimetaria*, *P. cyanescens*, *P. serbica*, *P. mairei*, *P. callosa*, and *P. semilanceata*.

Among the European species of *Psilocybe* only a few show bluish discolorations and are considered hallucinogenic, viz. *P. cyanescens* Wakef., *P. semilanceata* var. *caerulescens* (Cooke) Sacc. (=*P. cookei* Sing.), *P. serbica* Moser & Horak, and *P. fimetaria* (P. D. Orton) Watling.

Recently *P. cyanescens* has been reported from the Netherlands (Tjallingii, 1976), a record checked by the present authors. On studying, however, another gathering of a bluing *Psilocybe* collected in the Netherlands, they found the latter to represent an apparently as yet unknown species, which is described below.

The present paper is to be considered a precursor of a world monograph on *Psilocybe* in preparation by the senior author. He expresses his thanks to the Guggenheim Memorial Foundation for the grant enabling him to do this monographic work. Thanks are also due to Mr. D. M. Dring, Drs. H. S. C. Huijsman, Dr. M. Moser, Dr. E. Horak, Dr. R. Singer and Dr. R. Watling for making herbarium specimens available for comparison.

Psilocybe liniformans Guzmán & Bas, *spec. nov.*—Figs. 1–10

Pileus 10–25 mm latus, convexus, interdum subumbonatus, sordide ochraceo-brunneus, leviter olivaceo-tinctus, levis, hygrophanus, viscidus, avelatus. Lamellae adnexae, obscure argillaceae vel purpureo-brunneae, margine pallida, elastica. Stipes 14–30 × 1–2 mm, albidus vel pallide brunneus, basi caerulescens. Sporae (12–)13–14.5(–16.5) × 7.5–10 μm, ellipsoideae vel leviter inaequilaterales, luteo-brunneae. Pleurocystidia nulla. Cheilocystidia 22–33 × 5.5–9 μm, copiosa, lageniformia, longicollia, hyalina. Subhymenium subhyalinum, pigmento flavo-brunneo intercellulari irregulariter disposito. Epicutis gelatinosa. Fimicola. Typus: '*C. Bas 5512*, 10 Nov. 1970, Netherlands, Haamstede' (L; isotypus ENCB).

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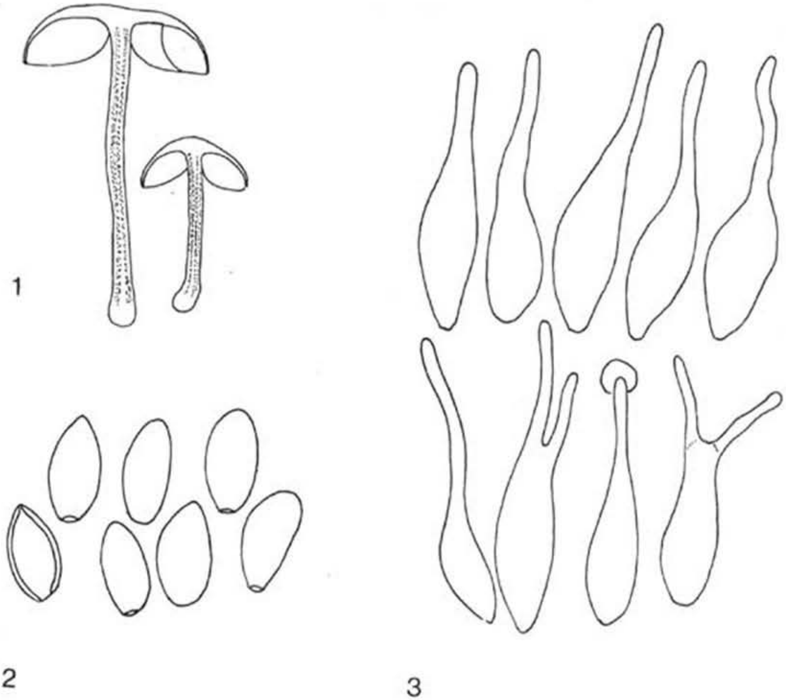

Figs. 1–3. *Psilocybe liniformans.* — 1. Fruit-bodies, × 1. — 2. Spores, × 1000. — 3. Cheilocystidia, × 1330 (Fig. 1. del. Bas. Figs. 2–3. del. Guzmán).

Pileus 10–25 mm in diam., convex to nearly plane, not papillate, sometimes slightly umbonate, hygrophanous, dull greyish ochraceous brown with slight olivaceous tinge (about Munsell* 10 YR 5/4 to 5/6), more reddish brown at centre (±7.5 YR 7/4), drying ochraceous buff (2.5 Y 7/6) with more brownish buff centre (±10 YR 5/8) and slightly greyish olivaceous buff margin (2.5 Y 6/4), in young specimens with a slightly bluish olivaceous tinge at margin, smooth, viscid, with separable pellicle, without any velar remnants. Lamellae adnexed, rather distant, broad, ventricose, fairly dark clay colour when young (between 10 YR 4/4 and 3/4) to purple brown (between 5 YR 3/2 and 3/3) with age; pallid, thickish edges detachable by a needle as an elastic thread. Stipe 14–30 × 1–2 mm, cylindrical but with up to 4 mm broad subbulbous base, hollow, whitish to very pale brownish with pale apex, with greenish blue tinge at base, finally greyish-greenish blue up to apex, pruinose-granulose above, concolorously fibrillose below. Context glassy, dull brown, later pallid in stem, with amber brown layer under surface of pileus and nearly

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* Munsell soil color charts. Munsell Color Company. Baltimore.

white core in stipe. Smell peculiar, strongly aromatic with foetid component when crushed. Taste weak, not unpleasant. Spore print not available.

Spores (12–)13–14.5(–16.5) × 7.5–10 μm, ellipsoid in face view, slightly inequilateral in side view, smooth, with thick wall yellowish brown in KOH and with distinct apical germ pore. Basidia 20–35 × 6–10 μm, 4-spored, hyaline in KOH, ventricose-subcylindrical, often with slight median constriction. Pleurocystidia absent. Cheilocystidia 22–33 × 5.5–9 μm, abundant, combined with underlying gelatinized hyphae to form a sterile, detachable, elastic thread, hyaline in KOH, lageniform, with more than 6 μm long and 1.5–2.5 μm wide neck, often forked, sometimes with hyaline, apical oil drop dissolvable in KOH. Subhymenium subhyaline, with yellow-brown pigment (observed in KOH) irregularly scattered among cells. Trama of lamellae regular, hyaline to brownish in KOH, made up of hyphae with elongate cells, without incrusting pigment. Epicutis gelatinized, consisting of embedded, parallel, thin, 1.5–3.3 μm wide, hyaline hyphae. Hypoderm formed by hyphae with hyaline, up to 15 μm wide elongate cells. Clamp-connections present.

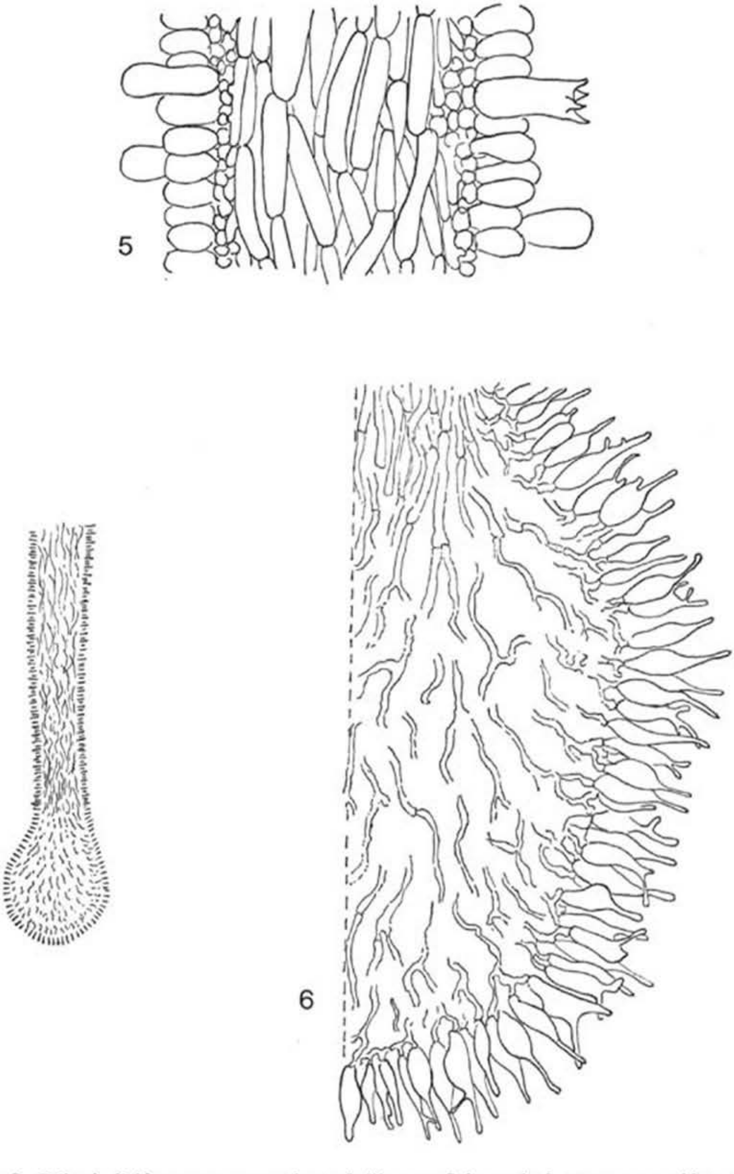
HABITAT & DISTRIBUTION.—Gregarious on horse dung on poor meadow in coastal dunes. Known only from type locality.

MATERIAL EXAMINED.—Netherlands, prov. Zeeland, Island of Schouwen, Haamstede, Duinhoeve, 10 Nov. 1970, *C. Bas 5512* (Type, L; Isotype, ENCB).

The species here described is close to *Psilocybe fimetaria* (P. D. Orton) Watling collected on horse dung also but with a well developed veil forming white fibrillose scales on and at the margin of the cap and a cortinate ring-zone on the stem, spores measuring 11–14(–15.5) × 6.5–8.5(–9.5) μm, and a non-gelatinized edge of the gill (see Orton, 1964: 59; type examined by senior author).

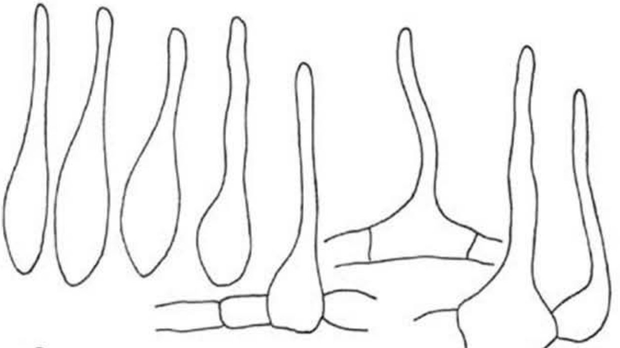
Psilocybe liniformans is also closely related to both *P. cyanescens* Wakef. and *P. serbica* Moser & Horak, but differs from the former in the shape of the cheilocystidia, and from the latter in the size of the spores. In fact, *P. cyanescens* has subfusiform-sublageniform cheilocystidia with necks not longer than 6 μm (Fig. 8). *Psilocybe serbica* has long-necked cheilocystidia arising from hyphae running parallel to the edge of the gill, as the senior author observed in the type (Fig. 7); this last feature is not mentioned in the original description (Moser & Horak, 1968: 140). The spores of *P. serbica* measure (9–)10–11(–13) × 5.5–6.5(–7.5) μm.

Psilocybe liniformans is also related to *P. mairei* Sing. (=*Hypholoma cyanescens* Maire, *Geophila cyanescens* (Maire) Kühn & Romagn.), known only from North Africa, a species which according to Malençon & Bertault (1970: 334) has spores measuring 11–12(–13.5) × 5.5–6.2 μm, and lageniform cheilocystidia measuring 30–40 × 6–8 μm. Also *P. callosa* (Fr. ex Fr.) Quél. and *P. semilanceata* (Fr.) Kumm. have some relationship with *P. liniformans*. They have cheilocystidia and spores similar in shape to those of the latter species but the size of these cells is different. *Psilocybe callosa* has spores measuring (9.5–)10–12(–14.5) × (6.5–)7–8.5μ m, and cheilocystidia measuring 20–45 × 4–7 μm (Fig. 6) as the senior author observed in Huijsman's specimens at L (see Huijsman, 1961: 91). *Psilocybe semilanceata* has (11–)12–14(–15.5) × 7–8 μm large spores, and 28–35 × 5–7 μm large cheilocystidia (Fig. 10) as the senior author observed in *Horak 63–41* at ZT (see Horak, 1968: 525). Moreover, both these species have a subumbonate or papillate pileus.



Figs. 4–6. *Psilocybe liniformans*, cross-sections of gill. — 4. Schematical, × 12.5. — 5. About 1 mm from edge, × 500. — 6. Edge of gill, × 500 (All Figs. del. Bas).

Psilocybe semilanceata var. *caerulescens* Cooke, raised by Singer (1973: 84) to specific rank under the name *P. cookei* Sing., probably is identical with the type variety of *P. semilanceata*. The senior author arrived at this opinion after studying several collections of *P. semilanceata* from Europe and North America, and the junior author agrees on the strength of many observations in the field. *Psilocybe semilanceata* has the base of the stem sometimes strongly, sometimes weakly, and sometimes not bluing at all.



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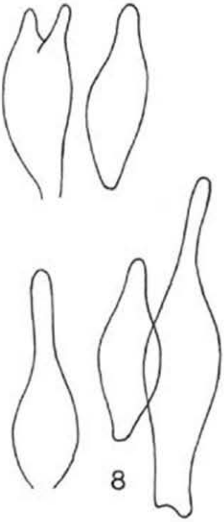

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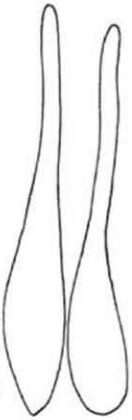

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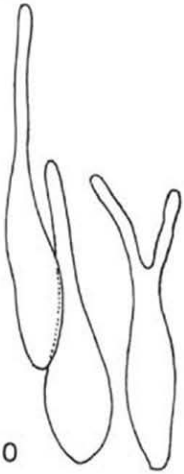

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Fig. 7. *Psilocybe serbica*, cheilocystidia, × 1330 (from type).
Fig. 8. *Psilocybe cyanescens*, cheilocystidia, × 1330 (from *Tjallingii 4 Nov. 1975*, L).
Fig. 9. *Psilocybe callosa*, cheilocystidia, × 1330 (from *Huijsman 28 Sept. 1960*, L).
Fig. 10. *Psilocybe semilanceata*, cheilocystidia, × 1330 (from *Horak 63–41*, ZT).
(All Figs. del. Guzmán.).

This variation pattern may be observed in a single lot of fruitbodies apparently growing on one and the same mycelium. Rarely there is also a slight bluish tinge visible on the margin of the cap of fresh specimens. In some populations of Mexican species of *Psilocybe* as *P. mexicana* Heim and *P. yugensis* Sing. & Smith a similar variation is present.

Because of the strong relationships with hallucinogenic *Psilocybe* species it is very probable that also *P. liniformans* contains psilocybine.

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NOTES ON HYGROPHORUS—II

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(With 36 Text-figures and Plate 20)

Hygrophorus (Hygrocybe) marchii Bres. and four closely related species are described, and a key to this group of species is given. One species is described as new, viz. *Hygrophorus phaeococcineus*.

Hygrophorus subsection *Coccinei* Bat. emend. Singer comprises brightly coloured species with broadly adnate gills and a dry, glabrous or somewhat fibrillose cap without squamules or a gelatinous pellicle (Singer, 1951: 152; Arnolds, 1974a: 169). This subsection includes some small-sized species with a cap less than 50 mm across, a stem less than 6 mm wide and, at least in young fruit-bodies, a red colour to the cap. These species are indicated below as the group of *Hygrophorus marchii* Bres. Among others *H. coccineus* (Schaeff. ex Fr.) Fr. is excluded from this group because of its larger size.

In recent years *H. marchii* has been described by many authors (see p. 244). As already observed by Singer (1969: 22) there are important discrepancies between several of these descriptions.

In order to assess the taxonomic significance of these differences I have studied a number of collections of this group from both Europe and the U.S.A. Besides *H. marchii* other European members of this group are *H. strangulatus* and *H. substrangulatus*, both described from Great Britain by Orton (1960: 267, 269). In addition a species already known to mycologists in the Netherlands for twenty years, is described here as *H. phaeococcineus* sp. nov. For the meaning of some terms and abbreviations used in this paper the reader is referred to my earlier note on *Hygrophorus* (Arnolds, 1974b).

I am very much indebted to Dr. C. Bas (Leiden), Dr. J. van Brummelen (Leiden), and to Mr. P. K. C. Austwick (London) for improving and correcting this paper. Thanks are also due to Mr. M. Bon (Lille), Drs. H. S. C. Huijsman (Beilen), Mr. P. D. Orton (Rannoch Station, Gr.-Br.), Dr. L. R. Hesler (Knoxville, U.S.A.), and Dr. R. Watling (Edinburgh) for sending me valuable collections and information.

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In the *H. marchii*-group the presence or absence of a constriction in the middle of the spores is frequently used as a key character. At the moment I find it difficult to decide on the taxonomic significance of this character, as I have not seen a single specimen of this group in which all the spores are constricted. On the other hand in only a few specimens constricted spores are completely lacking. This makes it necessary to determine the percentage of the spores in each preparation that are constricted. There are two complications. Firstly there are many spores with a shape intermediate between ellipsoid-oblong and constricted, and secondly the degree of constriction of a single spore depends on the side from which it is observed.

I have seen constrictions of spores more often in front-view than in side-view. The latter type seems to me more constant and of greater taxonomic importance, so that I have used this character in my key and descriptions. For the moment it is possible to distinguish two groups of taxa: one in which many spores are constricted (40–75% of the spores in side-view) and another in which only a few constricted spores occur (0–20% in side-view). Only in *H. substrangulatus*, otherwise characterized by large spores, do intermediate forms seem to occur regularly.

In certain other species of *Hygrophorus* the occurrence of constricted spores in part of the collections has not been used as a reason for distinguishing separate taxa, e.g. in *Hygrophorus ceraceus* (Wulf. ex Fr.) Fr. (Arnolds 1974a: 204, fig. 183; Orton 1960: 251) and *H. insipidus* (J. Lange) Lund. apud Lund. & Nannf. (Arnolds 1974a: 222, fig. 205; Orton 1960: 251).

Other problematic characters in the *H. marchii*-group are the degree of viscidity of the cap and the microscopical structure of the pileipellis. Both are influenced by climatological conditions and by the age of the carpophores. Moreover the thickness of the pileipellis is difficult to determine because a sharp border line between this tissue and the trama of the cap cannot be drawn, while measurements on dried specimens are strongly influenced by the quality of drying. In the following key and in the descriptions I have indicated as pileipellis the superficial layer of narrow hyphae (1.5–6 μm) as distinct from the broader hyphae underneath (5–15 μm), as seen in well-dried specimens.

In all specimens described here I have observed a more or less clearly differentiated layer between the pileipellis and the subparallel, radially disposed hyphae of the pileitrama. This tissue could be called a subcutis, using the terminology of Moser (1967). According to Bas (1969: 327) it is better to use the term '*subpellis*', analogous to 'pileipellis'. These are topographical terms free from etymological connections with descriptive terms like 'cutis'. The subpellis here consists of irregularly compacted interwoven hyphae with short, somewhat inflated cells, giving this tissue on radial section sometimes an almost cellular appearance as is the case in a hypodermical structure (e.g. Fig. 34).

In fresh specimens this layer contains the greatest concentration of vacuolar pigments. Of all authors describing *H. marchii*, only Bon (1974) pays attention to this special structure beneath the pileipellis. For the moment I cannot judge the taxonomic importance of this character for the delimitation of the *H. marchii*-group within

Hygrocybe. I observed a differentiated subpellis also in some collections of *H. miniatus* (Fr.) Fr. (Arnolds, 1974a: 184, 188).

In the field all species of the *H. marchii*-group can easily be confused with representatives of subsection *Squamulosi* Bat., especially with *H. miniatus* (Fr.) Fr. However, some fundamental microscopic differences exist, as is mentioned in the discussion on *H. strangulatus* below.

As a result of my investigations the following key has been prepared:

KEY TO THE SPECIES IN THE *Hygrophorus marchii*-GROUP IN EUROPE (INCLUDING ONE NORTH AMERICAN SPECIES)

1a. Pileipellis composed of thin, gelatinized hyphae, 1.5–5 µm broad (Figs. 10, 11, 15); cap slightly viscid at first. Spores 6.5–8.5(–10) × 3.5–5 µm 2

b. Pileipellis composed of broader, non-gelatinized hyphae, (2.5–)3–7.5 µm broad (Figs. 28, 34); cap dry. Spores often larger, 6.5–11.5(–12.5) × 3.5–6.5(–7) µm 3

2a. Spores in side-view not or rarely constricted (less than 20%; Figs. 3–6). Pileipellis rather compactly interwoven, 40–100(–120) µm thick (Figs. 10, 11) . . . . *H. marchii*, p. 241

b. Spores in side-view often constricted (more than 50%; Figs. 12, 13). Pileipellis loosely interwoven, 25–40 µm thick, with stronger gelatinized hyphae (Fig. 15) *H. marchii* sensu Hesler & Smith, p. 245

3a. Cap first scarlet, blood red or purplish red, discolouring orange-yellow with age, in well-dried fruit-bodies turning typically dark brown or dark orange-brown. Superficial hyphae of cap in fresh fruit-bodies with brown vacuolar pigment, in part also with greyish granulae and clots; brown pigment persistant in dried specimens and in KOH 5%. Spores (7–)7.5–11(–11.5) × (3.5–)4–6.5(–7.5) µm, not or only a small part (less than 20%) constricted in side-view (Figs. 21–24). Basidia relatively short: (26.5–)28.5–47.5(–49) × (4.5–)5.5–9(–9.5) µm (Fig. 26) . . . . *H. phaeococcineus*, p. 247

b. Cap first vermilion or orange-red, discolouring orange-yellow with age, in well dried specimens turning ochre or pale orange-brown. Superficial hyphae of the cap colourless or with pale yellow, vacuolar pigment, colourless in KOH 5%. Spores 6.5–11.5(–12.5) × 3.5–6.5(–7.5) µm, mostly in greater part (40–70%) constricted in side-view. Basidia (34–)36–63.5(–65.5) × (5.5–)6–10.5(–12.5) µm. 4

4a. Spores 6.5–10(–11.5) × 3.5–5(–5.5) µm, averages 7.5–9.3 × 3.7–4.7 µm; many (40–70%) clearly constricted in side-view (Figs. 31, 32). Basidia (5.5–)6–8 µm broad (Fig. 33) *H. strangulatus*, p. 250

b. Spores (8–)9–11.5(–12.5) × 4.5–6.5(–7.5) µm, averages 10.4–10.9 × 6.0–6.3 µm, in side-view rather frequently weakly constricted (Figs. 16, 17). Basidia (7.5–)8–10.5(–12) µm broad (Fig. 18). . . . . *H. substrangulatus*, p. 253

HYGROPHORUS MARCHII Bres.[1]—Plate 20c; Figs. 1–11

Hygrophorus marchii Bres., Ic. Mycol. 7: 343. 1928. — *Hygrocybe marchii* (Bres.) Sing., *in* Lilloa 22: 153. '1949' [1951].

Misapplication.—*Hygrophorus marchii* sensu Hesler & Smith, North American species of *Hygrophorus*: 209. 1963.

COLOURED ILLUSTRATIONS.—Bresadola, l.c.; Reid, Col. Ic. rare interest. Fungi 3: pl. 18a. 1968.

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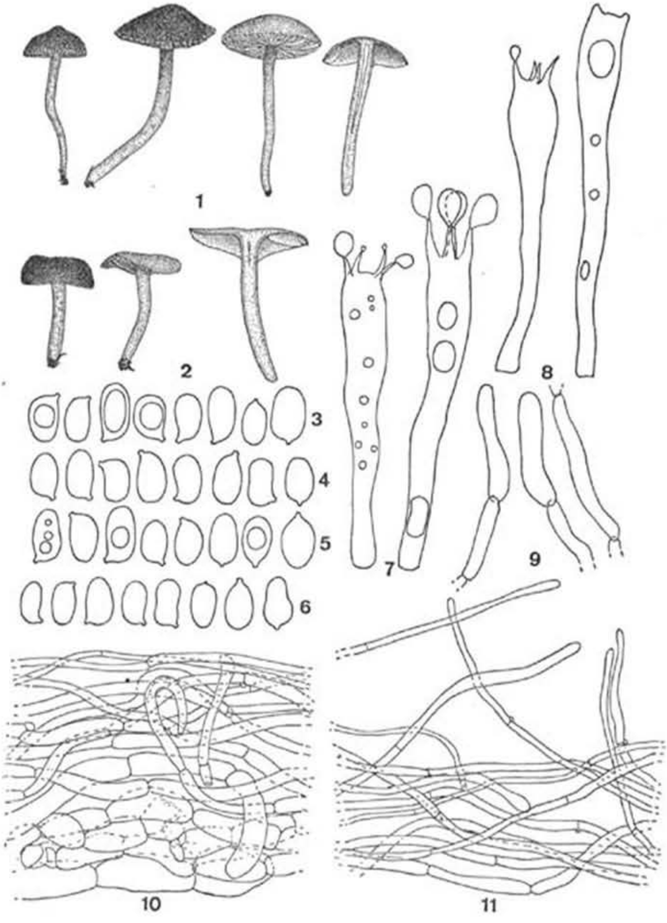
[1] The description is based on the collections available from the Netherlands.



Figs. 1–11. *Hygrophorus marchii* Bres. — 1–2. Carpophores, × 1/2. — 3–6. Spores, × 1000. — 7–8. Basidia, × 1000. — 9. Elements of trama of gills, × 250. — 10. Radial section of pileipellis and subpellis, × 500. — 11. Radial section of pileipellis, × 500. (Figs. 1, 3, 7, 9 from *Arnolds 3278*; Figs. 2, 10 from *Arnolds 3067*; Fig. 4 from *Jensen, 29 Oct. 1960* (*Hesler 23.940*); Figs. 5, 8 from *Huijsman 67.450*; Figs. 6, 11 from *Henderson 4174*).

Cap 15–40 mm wide, first broadly flattened conical, then expanded, sometimes slightly obtuse umbonate, often with slightly wavy, lobed, finally sometimes reflected margin, clearly hygrophanous, when young and moist scarlet, vermilion or orange-red (M. 8B8, 9B8, 10B8)[2] with extreme margin bright orange-yellowish, gradually discolouring to orange, orange-yellow or pale orange-ochre (M. 5A7, B5, 6A7, 7A7) when drying and by ageing; non-striate or striate at outmost margin only (max. 4 mm); surface especially of young caps greasy or slightly viscid when moist, drying to glabrous or at centre finely adpressedly hairy. Gills (L 17–25, l 1–5) broadly adnate or slightly decurrent, often slightly ventricose, up to 7 mm broad, thick and distant, brittle; colour varying from pale yellow to orange-yellow, orange, orange-red or rose-red, always with broad paler edge. Stem 26–54 × 3–6 mm (–8 mm when compressed), l/b 6–14.5, rather slender, stuffed or hollow, straight, slightly curved or somewhat flexuose, attenuated downwards, sometimes compressed, vermilion or orange-red with lighter orange or yellowish base, or entirely orange- or chrome yellow, shiny when moist but not viscid, smooth or slightly striate when dry. Flesh in cap thin, rather fragile, concolorous with surface of cap; in outer layer of stem also of the same colour, but in spongy centre yellowish. Smell and taste none or slightly sweetish. Well-dried specimens light orange, light orange-brown or ochre-brown (M. 4A4–5A4, 5A4, 5A6, 5B5, 5B6).

Spores [30/3/2] 7–8.5(–10) × 4–5 μm, l/b 1.5–2.0, ellipsoid-oblong or ovoid-oblong, sometimes slightly curved, more rarely (<10%) slightly constricted in face-view, with moderately large oblique apiculus, colourless in water and alkaline solutions, yellowish in Melzer's (Fig. 3). Basidia [30/3/2] (39.5–)41–53(–56.5) × (6–)6.5–8.5(–9.5) μm, l/b 5.2–7.1(–7.9), rather slender or slenderly clavate, 4-spored, sometimes a few 2- or 3-spored (then a minor part of the spores longer than 8.5 μm; Fig. 7). Pleuro- and cheilocystidia not seen. Trama of gills subregular, composed of subparallel hyphae with long chains of moderately long, cylindrical or somewhat ventricose cells with obtuse ends, measuring [25/3/2] (45–)52–122(–143) × (4.5–)7.5–15(–16.5) μm, l/b 4.2–10.9(–15.6) (Fig. 9). Pileipellis a cutis, 40–70 μm thick, composed of mainly radially oriented, prostrate hyphae, just beneath surface loosely interwoven, colourless, slightly gelatinous and often with scattered upright ends; all hyphae slender with long cylindrical cells, 1.7–5(–7) μm broad, not constricted at septa; more downward gradually passing into hyphae of trama (Fig. 10). Pileitrama almost regular, beneath pileipellis slightly interwoven with short cylindrical cells, 5–18(–22) μm broad (a subpellis); in fresh specimens with brightly yellow vacuolar pigment; beneath the subpellis with more slender subparallel, cylindrical hyphae, 5–14.5 μm broad, with pale yellow vacuolar pigment or colourless. Stipitepellis a thin dry cutis of non-gelatinous hyphae of 1.5–5.5 μm broad. Clamps observed in most collections at base of basidia.

HABITAT.—In the Netherlands rare; only known from two dike-slopes grown with short mossy grassland extensively grazed by cows and not treated with fertilizers, on dry, rather rich, loamy soil. October-November.

COLLECTIONS EXAMINED.—THE NETHERLANDS: prov. Friesland, Island of Terschelling, dike near Midsland, 4 Nov. 1973, *Arnolds 3067* (L, WBS); prov. Gelderland, Wilp, dike along the river IJssel, 26 Oct. 1974, *J. Piepenbroek & G. Piepenbroek Grooters* (*Arnolds 3278*; L, WBS).

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[2] Colour codes are according to Kornerup & Wanscher, Methuen Handbook of Colour, 2n Ed., 1967. London.

Studies on some dried collections from other European countries resulted in the following additional microscopic features:

Spores [120/12/12] (6–)6.5–8.5(–10) × 3.5–5(–6) μm, averages 6.9–8.4 × 3.9–5.0 μm, l/b 1.5–2.1(–2.2), ellipsoid-oblong or ovoid-oblong, in some collections frequently slightly curved (Fig. 4), not or weakly constricted in a small minority (at most 20%; Figs. 4–6). Basidia [52/9/9] (40–)41–58(–60.5) × (5.5–)6–8.5(–9) μm, l/b 5.5–9.0(–10.4), rather to very slenderly clavate, in all specimens mostly 4-spored, rarely some 2- or 3-spored (Fig. 8). Cheilo- and pleurocystidia none. Pilcipellis a well-developed cutis or slightly gelatinized ixocutis 40–100(–120) μm broad, hyphae 1.5–5(–6.5) μm thick, in upper layers often slightly gelatinous (Fig. 11), otherwise as described from the Netherlands' collections above.

COLLECTIONS EXAMINED.—FAEROES, Syderö, ved Lopra Hvalstation, 28 Aug. 1938, *F. H. Möller s.n.* (C).

DENMARK: Kejlsö, Tegnet, 12 Oct. 1941, *F. H. Möller s.n.* (C); Sjaelland, Dyrehave, Jaegersborg, 29 Oct. 1960, *J. P. Jensen* (*Hesler 23940*; TENN); Jylland, 9 Oct. 1971, *M. Lange s.n.* (C); Jutland, Hvalpsund, 22 Oct. 1969. *J. Barkman 9121* (WBS).

FRANCE: Franche-Comté, Lougres près de Montbéliard, 1 Nov. 1967, *H. S. C. Huijsman 67.450* (L); St. Valéry la Garenne, 24 Oct. 1974, *M. Bon 72102402* (herb. Bon); Creuse?, 18 Oct. 1971, *P. Joly* (*M. Bon 71101804*; herb. Bon).

GREAT BRITAIN: Tomich, 27 Aug. 1957, *R. Watling 114C* (E); Loch an Eilean, 7 Sept. 1958, *D. M. Henderson 4174* (E); Mull, Ben Mohr, 14 Sept. 1968, *D. M. Henderson 9107* (E); St. Kilda, Mollach Bi, 8 Sept. 1967, *R. Watling 5972* (E).

SWITZERLAND: Neuchâtel, Les Pontins, 10 Sept. 1959, *H. S. C. Huijsman s.n.* (L); Neuchâtel, Boudry, 17 Oct. 1965, *H. S. C. Huijsman s.n.* (L).

It is remarkable that so many authors have extensively described *H. marchii* in the last decades. Without trying to be complete I refer to Möller, 1945; Favre, 1955; Haller, 1956; Orton, 1960; Svrček, 1962; Hesler & Smith, 1963; Reid, 1968; Singer, 1969; Bon, 1974. Not all their descriptions are identical with the one given above.

Of the descriptions of species in the *H. marchii*-group given in this paper, the one above is the only one that fully agrees with the original diagnosis and plate by Bresadola (l.c.). Important characters in this respect are the vermilion or orange-red, first slightly viscid cap and the non-constricted spores (cf. spores pictured by Bresadola). It seems that there is no material left of *H. marchii* collected by Bresadola himself. Such collections are lacking in the herbaria of Stockholm (S) and Beltsville U.S.A. (BPI) according to the informations kindly given to me by the directors.

According to the accounts in recent literature *H. marchii* seems to be a widespread and locally common mushroom in Western and Central Europe. It is rather variable in some characters, e.g. spore size. The smallest spores observed by me are in the British collection *Henderson 4174*, viz. (6.2–)6.5–7.3(–7.5) × 3.6–4.2 μm; the largest in the collection *Barkman 9121* from Denmark, viz. 7.6–8.7(–10.0) × 4.2–5.0(–5.2) μm. Reid (1968: 5) has already mentioned the variations in the descriptions of this species. However, there is no reason to distinguish different taxa on this basis, as demonstrated in a scatter diagram (Fig. 36).

Some variability also exists in the thickness of the pilcipellis and in the abundance of hyphae projecting upwards with hair-like ends. In some collections the latter are completely lacking (Fig. 10), in others upstanding hyphae are rather frequent (Fig. 11) like those figured by Bon (1974, Fig. 1 J). Both types grade into each other. The presence of erect hyphae is correlated with the macroscopic appearance of the cap, which then is hairy when dry.

Singer (1969) distinguished three concepts of *H. marchii*: sensu Orton (1960), sensu Favre (1955) and Möller (1945), and sensu Hesler & Smith (1963) respectively. I agree with him in separating the latter (see p. 000), but in my opinion *H. marchii* sensu Orton is identical with *H. marchii* sensu Favre and Möller. According to Singer (l.c.) the main difference between both concepts would be that Orton's fungus should have the cap transparently striate over one half of the radius, and Favre's fungus should not have striations at all. Singer concluded this from the fact that Orton (l.c.) did not mention in his key any difference in striation between *H. marchii* and *H. strangulatus*, whereas *H. strangulatus* should have a striate cap. However, Orton states in his description of *H. strangulatus* (1960: 266): 'when moist striate at margin only', which is also obvious from his figure 77. Favre (1955: 35) and Bresadola (1928: 343) both describe and depict *H. marchii* with a non-striate cap. Fruit-bodies without and with a short striation often grow together in the same locality.

HYGROPHORUS MARCHII sensu Hesler & Smith—Figs. 12–15

Hygrophorus marchii sensu Hesler & Smith, North American Species of *Hygrophorus*: 209–210, fig. 60. 1963.

For a complete macroscopic description and a photograph the reader may be referred to Hesler & Smith (l.c.). A study of two collections, kindly sent to me by Dr. L. R. Hesler, revealed the following microscopical features:

Spores [22/2/2] (6–)6.5–8(–8.5) × 3.5–4.5 μm, averages 7.1–7.5 × 4.1 μm, l/b 1.7–2.0(–2.1), ellipsoid-oblong, but for the greater part (more than 60%) slightly to strongly constricted in side- as well as in face-view, with a small acute apiculus (Figs. 12, 13). Basidia [17/2/2] (30–)32–46.5 × 5.5–7.5 μm, l/b (5.0–)5.2–7.2(–7.4), rather slenderly clavate with 4 sterigmata (Fig. 14). Pleuro- and cheilocystidia none. Trama of gills composed of subparallel hyphae c. 6–16 μm broad. Pileipellis a thin (25–40 μm), clearly differentiated ixocutis of repent and ascending, narrow, gelatinous hyphae 1.5–5 μm broad (Fig. 15). Trama of pileus consisting of radial subparallel hyphae 5.5–14 μm broad, but beneath the pileipellis rather strongly interwoven (a subpellis). Stipitepellis a thin dry cutis; superficial hyphae 1.7—5 μm broad. Clamps present at base of basidia.

COLLECTIONS EXAMINED.—U.S.A.: California, Trinidad, 3 Dec. 1956, *A. H. Smith 56213* (TENN); Cheboygan Co., Colonial Point, Douglas Gate, 4 July 1974, *A. H. Smith 32421* (MICH).

I found the spores significantly smaller than the size range given by Hesler & Smith (l.c.: 209), viz. 7–10 × 3.5–5 μm. Singer (1969: 22) observed still larger spores: 8.8–10.2 × 4.3–5 μm. This difference is possibly due to rather great variation between some collections. It is also remarkable that Hesler & Smith mention the spores being 'at times faintly' constricted, whereas Singer describes them as 'often (although by far not all) slightly constricted in the middle'. I found the majority of spores clearly constricted.

The abundance of constricted spores forms the main difference with *H. marchii* Bres., as described by various European authors. Moreover the pileipellis is thinner but at the same time more clearly gelatinous. The cap seems to flatten sooner and to be darker red (blood red) in young fruit-bodies (Hesler & Smith, l.c.).

The spores are much like those of the European *H. strangulatus* Orton (see p. 252), but *H. marchii* sensu Hesler & Smith is much more robust and has an ixocutis instead


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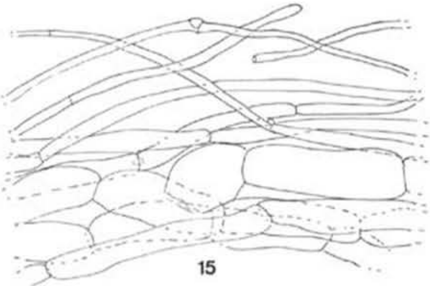
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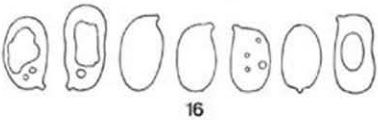
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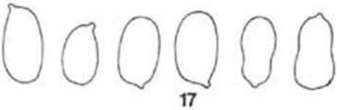
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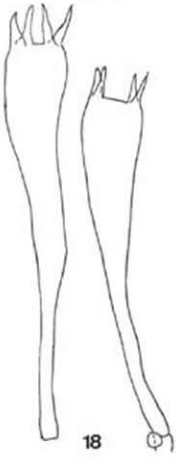
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Figs. 12–15. *Hygrophorus marchii* sensu Hesler & Smith. — 12–13. Spores, × 1000. — 14. Basidia, × 1000. — 15. Radial section of pileipellis and subpellis, × 700. (Figs. 12, 14, 15 from *Smith 56213*; Fig. 13 from *Smith 32421*)

Figs. 16–18. *Hygrophorus substrangulatus*. — 16–17. Spores, × 1000. — 18. Basidia, × 1000. (Figs. 16, 18 from *Orton 2365*; Fig. 17 from *Orton 477*) of a thin dry cutis. So it seems that *H. marchii* sensu Hesler & Smith has to be redescribed under a new name.

Hesler & Smith (l.c.) think that their concept of *H. marchii* is very close to that of *H. flavescens* (Kauffm.) Smith & Hesl. I do not agree with this point of view. The trama of the gills of the latter species has quite another structure. It consists of strictly parallel hyphae with very long and broad, tapering cells 450–1300 × 9.5–30 µm (Arnolds 1974a: 146, Figs. 110, 111). Besides the basidia are much broader, and the outermost hyphae on the stem of *H. flavescens* are very slender and gelatinous. In my opinion *H. flavescens* belongs to another section of *Hygrophorus*, viz. sect. *Hygrocybe* (Holotype: *Hygrophorus conicus* (Scop. ex Fr.) Fr.). (See Arnolds, 1974a: 144.)

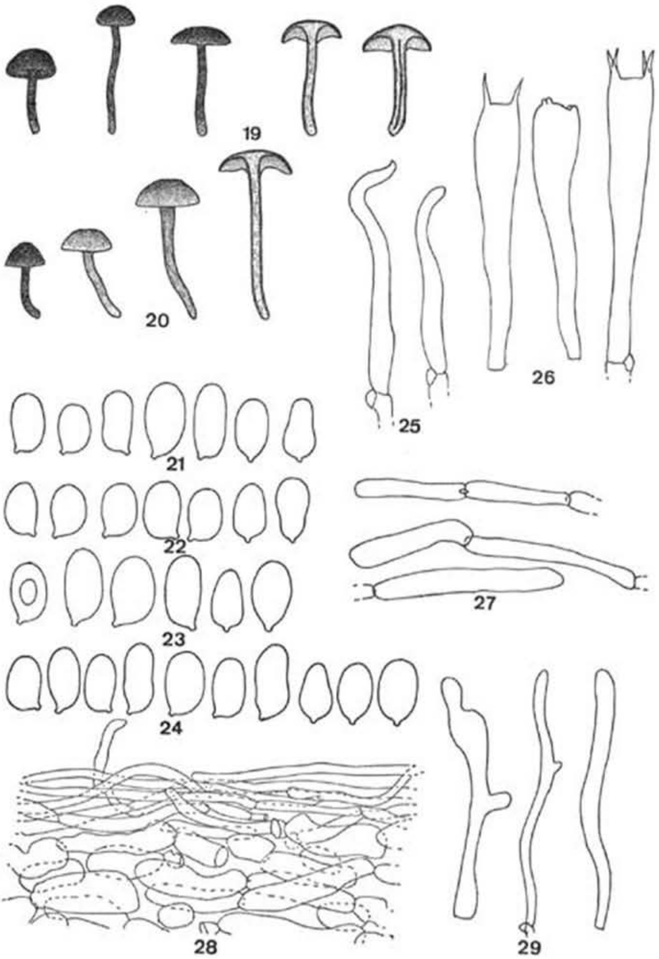
Hygrophorus phaeococcineus Arnolds, *spec. nov*

Plate 20b; Figs. 19–29

Pileus (6.5–)10–40(–56) mm latus, semiglobatus vel convexus, dein leviter convexus vel expansus, hygrophanus, coccineus vel sanguineus vulgo margine aurantius vel flavus, posterior totus aurantio-luteus, in exsiccata vulgo brunnescens, glaber vel leviter tomentosus. Lamellae (L 14–32, l 1–3(–5)) late adnatae vulgo dente decurrentes, subdistantes, fragiles, primo pallide miniatae vel flavae, dein salmonicolores, ceraceae vel pallide aurantio-luteae. Stipes (12–)20–60 × 1.5–4(–5) mm, deorsum aequalis vel attenuates, vulgo leviter flexuosus, fragilis, primo totus vel ad apicem coccineus vel aurantio-miniatus, dein aurantius vel ceraceus, siccus, glaber, basis albo tomentosus. Caro fragilissima, sub cuticulae pilei et stipitis concolor, intus flava vel pallide aurantia. Odor et sapor nulli. Sporae (7–)7.5–11(–11.5) × (3.5–)4–6.5 (–7.5) µm, l/b (1.4–)1.6–2.1(–2.3), ellipsoideo-oblongae vel ovoideo-oblongae, raro pro parte minoris leviter strangulatae. Basidia (26.5–)28.5–47.5(–49.0) × (4.5–)5.5–9(–9.5) µm, vulgo 4 sporigera, raro pro parte minoris 3 vel 2 sporigera. Lamellarum acies fertilis interdum paucis cystidiis cylindricis, (18–)25–35(–49) × 1.5–2.5(–3) µm. Lamellarum trama subregularis, cellulis 46.5–180(–230) × (4.5–)6.5–15.5(–20) µm. Pileipellis cutiformis, 15–35(–45) µm latus, hyphis 3.5–6.5 µm latis, cylindricis, interdum pro parte erectis. Pileitrama sub pileipellis irregularis, cellulis, inflatis, 5–9 µm latis. Inter musci et graminos ad terram in locis humidis et acidis. Holotypus: 'Vlieland, Kroon's Polders, 31 Oct. 1976, *Arnolds 3710*' (in herb. Biol. Stat. Dr. W. Beyerinck, Wijster=WBS; isotypus L).

ETYMOLOGY: phaeus, dark; coccineus, bright red or scarlet.

Cap (6.5–)10–45(–56) mm wide, first semiglobate or strongly convex, then slightly convex, rarely flattened, rather hygrophanous; bright scarlet or dark blood red at first (M. 9B8, 9C8, 10C8, 10D8, 11C8), often with narrow orange or yellow margin, drying pinkish red; gradually discolouring orange-red, orange or orange-yellow (M. 6A7, 6B8, 7B8, 8A8–B8), finally mostly light orange-brown or ochre-brown (M. 5C8, 6C8, 7C7); when moist slightly greasy, often appearing waxy, as covered by a thin, greyish coating, drying smooth or very faintly golden-yellow to orange adpressedly velvety-hairy; margin not striate or rarely short-striate when moist. Gills [L 14–32, l 1–3(–5)] broadly adnate, mostly with decurrent tooth, thick, subdistant, very brittle, when young at most pale rose-red (M. 7B6, 8A6, 8B6, 10A7) with narrow pinkish yellow or sulphur yellow edge, entirely passing into light salmon pink, pinkish wax yellow or light yellow-orange (M. 5A3, 5A6, 6A4–A6, 7A5). Stem (12–)20–60 × 1.5–4(–5) mm, l/b (3–)6–18, slender, stuffed or slightly hollow, mostly somewhat curved, generally tapering downwards, very fragile, scarlet or orange-red



Figs. 19–29. *Hygrophorus phaeococcineus*. — 19–20. Carpophores, × 1/2. — 21–24. Spores, × 1000. — 25. Basidioles, × 1000. — 26. Basidia, × 1000. — 27. Elements of trama of gills, × 250. — 28. Radial section of pileipellis and subpellis, × 500,. — 29. Cheilocystidia, × 1000. (Figs. 19, 22, 28 from *Kalff, 20 Aug. 1961*; Figs. 20, 24 from *Arnolds 644*; Figs. 21, 26, 29 from *Arnolds 3650* (Holotype); Figs. 23, 25 from *van de Bergh, 7 Oct. 1969*)

(M. 8A8, 9B8, 10B8) at first, at least at apex, gradually discolouring orange, orange-yellow or wax yellow (M. 4A5, 5A5–A8, 6A8) from base upward; extreme base white tomentose; surface glabrous or finely striate, dry on the touch. Flesh very brittle, beneath the surface of the cap concolorous, otherwise egg or lemon yellow; outer tissue of the stem coloured like surface; in the centre fibrous, pale orange or pale yellow. Smell and taste absent. Well-dried specimens remarkably dark brown or purplish brown (M. 5E6, 5E7, 6E6, 7E6), also dull orange- or ochre brown (M. 5C7, 5D6, 5D7, 6D7) after some years.

Spores [150/13/11] (7–)7.5–11(–11.5) × (3.5–)4–6.5(–7.5) μm. averages 8.0–10.3 × 4.4–5.6 μm, l/b (1.4–)1.6–2.1(–2.3), in side-view ellipsoid-oblong, ovoid-oblong or subcylindrical, often slightly curved, rarely (at most 20%) slightly constricted in the middle; in front-view mostly broader ovoid, sometimes pyriform or constricted (Figs. 21–24). Basidia [90/12/12] (26.5)28.5–47.5(–49) × (4.5–)5.5–9(–9.5) μm, l/b (3.6–)4–6.7(–8.7), moderately to rather slenderly clavate, 4-spored, sometimes a few 3- or 2-spored (Fig. 26); basidioles sometimes frequent, approximately cylindrical (Fig. 25). Cheilocystidia present in some collections but not constant in all specimens, scattered, hair-like to cylindrical or shaped like basidiolae, rather frequently forked, about (18–)25–35(–49) × 1.5–2.5(–3.5) μm (Fig. 29). Pleurocystidia absent. Trama of gills subregular, composed of slightly interwoven hyphae with cylindrical or somewhat inflated cells with rounded ends, about 46–180(–230) × (4–)6–15(–20) μm (Fig. 27). Pileipellis a thin dry cutis, 15–45 μm thick, consisting of a few layers of narrow repent hyphae with a few scattered erect hair-like ends, 3.5–6.5(–8) μm wide, with brownish vacuolar pigment and often with grey-brown intracellular granulae and clots, often agglutinated in older fruit-bodies and then with very obscure structure (Fig. 28). Pileitrama beneath the pileipellis forming a subpellis consisting of compact, irregularly interwoven hyphae with inflated cells 4–13 μm broad, in fresh specimens with red to orange-yellow vacuolar pigment; beneath this layer subparallel radial hyphae with cylindrical or slightly inflated cells (6–)9–20(–25) μm broad, with pale yellowish vacuolar pigment. Stipitepellis hardly differentiated, with parallel longitudinal narrow hyphae, 3–5 μm broad. Stipitetrama subregular, consisting of hyphae with cylindrical cells with rounded ends, 4.5–12 μm broad. Clamps sometimes not found but in most specimens present at base of basidia; also seen at hyphae of pileipellis and trama of gills.

HABITAT.—Known from several mossy and grassy valleys in the coastal dunes, on moist, acid, sandy soil poor in lime (pH 4.5–5), rich in humus, and from a few mossy and grassy spots on moist acid peat or peaty sand in the inland (cf. Arnolds, 1974: 92, map 20). August-October.

COLLECTIONS EXAMINED.—THE NETHERLANDS: prov. Friesland, Island of Vlieland, Kroon's Polders, 31 Oct. 1976, *E. Arnolds 3710* (holotype herb. Biol. Stat. Dr. W. Beyerinck, Wijster: WBS; isotype L); Island of Terschelling, Midsland, 9 Sept. 1954, *Jansen-v. d. Plaats s.n.* (L); prov. Gelderland, Overasselt, Hatertse Broek, 26 Sept. 1954, *Exc. Ned. Mycol. Ver.* (L); 20 Aug. 1961, *J, Kalff s.n.* (L); Winterswijk, Korenburgerveen, 29 Sept. 1973, *C. Bas 6174* (L); prov. Noord-Holland, Petten, Derde Korfwater, 7 Oct. 1969, *F. v. d. Bergh s.n.* (L); Bergen, Verbrande Pan, 5 Oct. 1969, *E. Arnolds 347* (L); Island of Texel, De Geul, Calamagrostis-valley, 30 Oct. 1970, *E. Arnolds 579* (L); 30 Oct. 1971, *E. Arnolds 644* (L); Island of Texel, De Geul, path in the dunes, 9 Oct. 1969, *E. Arnolds 380* (L); Island of Texel, De Geul, grassland in the dunes, 9 Oct. 1969, *E. Arnolds 385* (L); prov. Noord-Brabant, Deurne, Helenaveen, 15 Oct. 1958, *C. Bas 1583* (L); Eindhoven, Liessel, 9 Oct. 1965, *E. Kits van Waveren s.n.* (L).

This fungus has been known to mycologists in the Netherlands for many years but was at first usually mistaken for small specimens of *H. coccineus*. Dr. C. Bas (Rijksherbarium, Leiden) recognized already in 1954 the great difference in size and stature between *H. phaeococcineus* and the latter, and found some peculiarities, e.g. the browning of dried specimens. On account of these features he already noted a provisional name, *H. phaeococcineus*, on the wrappers.

Probably this species is most related to *H. marchii*. Macroscopic differences with the latter are the dark red colour of the cap and the more slender stem. Besides, *H. phaeococcineus* is the most fragile of all species treated here, and the only one turning brown after drying (especially adult specimens). Microscopic differences with *H.marchii* are the thinner, dry pileipellis and in general also the occurrence of larger spores and shorter basidia. Although some overlap exists between both species in size of spores (Fig. 36), basidia, and fruit-bodies, the total complex of characters certainly justifies the distinction of two taxa. In the Netherlands an ecological difference alxo exists: whereas *H. phaeococcineus* has been always found on moist, peaty, acid soils, *H. marchii* grows in grasslands on dry, loamy, subneutral soils. Perhaps the records of *H. marchii* for Great Britain refer in part to *H. phaeococcineus*. From the published descriptions of *H. marchii* the one by Orton (1960: 252) comes closest to the species described above. However, I could not find proof for this supposition in the few British collections of *H. marchii* I was enabled to examine. Orton studied one collection of *H. phaeococcineus* many years ago, and concluded in a letter to Bas (16 Apr. 1961): 'I agree this species is not in my key'. Also Hesler studied some dried specimens in preparing the book on *Hygrophorus* in North America, and stated in a letter (7 Feb. 1961) that he did not know the species.

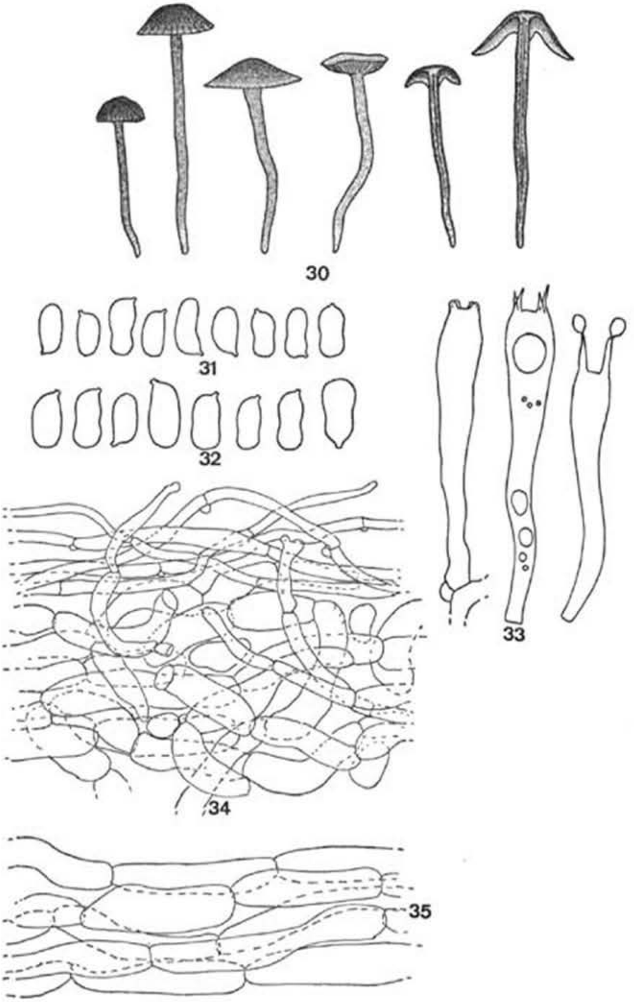
It could be useful to study the relationship between *H. phaeococcineus* and *Hygrocybe mexicana* Sing. (Singer 1958: 225; Hesler & Smith 1963: 181). The latter seems to be related, also by presence of remarkably short basidia. However, on account of some minor discrepancies in the short description of *H. mexicana* (e.g. the cap is strongly striate) and a different distributional pattern, it seems improbable that these two taxa are conspecific.

HYGROPHORUS STRANGULATUS P. D. Orton—Plate 20a; Figs. 30–35

Hygrophorus strangulatus P. D. Orton *in* Trans. Br. mycol. Soc. **43**: 266. 1960. — *Hygrocybe strangulata* (P. D. Orton) Svrček *in* Česká Mykol. 16: 167. 1962.

MISAPPLICATION.—*Hygrophorus strangulatus* sensu Reid *in* Nova Hedw. **15** (Suppl.; Col. ic. rare interest. fungi **3**): 6, pl. 18 b, fig. 5. 1968 (=*H. miniatus* (Fr.)Fr.).

Cap 8–32 mm broad, first convex or broadly flattened conical, gradually less convex or expanded, rarely flattened or slightly depressed, strongly hygrophanous, when moist in young fruit-bodies scarlet, vermilion or orange-red (M. 8B8, 9B8) with narrow orange or orange-yellow margin, gradually discolouring orange, orange-yellow (M. 5A8, 6A8), finally dull light brownish orange when old (M. 5B6); drying pale orange (M. 5A3, A4) or even light yellow (M. 4A4) from the centre outwards; when moist the margin shortly translucently striate (up to 1/4 R of cap);



Figs. 30–35. *Hygrophorus strangulatus*. — 30. Carpophores, × 1/2. — 31–32. Spores, × 1000. — 33. Basidia, × 1000. — 34. Radial section of pileipellis and subpellis, × 500. — 35. Radial section of pileitrama, × 500. (Fig. 30 from *Arnolds 544*; Figs. 31, 33, 34, 35 from *Arnolds 3486*; Fig. 32 from *Kits van Waveren, 6 Oct. 1961*).

surface glabrous or slightly greasy when moist, not viscid; when dry dull and especially at centre often covered with very fine hairy fibrils, giving a velvety impression, sometimes very fine golden scurfy but never distinctly squamulose or scaly. Gills (L 17–23; l 1–3(–5)) broadly adnate, often with tooth, or short decurrent, not or slightly ventricose, up to 5 mm broad, rather thick, distant, first pale yellowish, then pale orange (M. 5A4) with broad yellowish edge, finally mostly darker pinkish orange (M 6A6) or orange-red with narrower sulphur yellow or orange-yellow edge. Stem (14–)23–60(–72) × 1.5–4 mm, l/b (4.0–)9.3–18.0, slender, often somewhat curved, attenuated downwards or equal, stuffed, first orange-red or orange, with base more yellow-orange, later often becoming entirely orange- or chrome yellow (M. 3A7, 5A7) from base upwards, sometimes whitish or whitish tomentose at base; surface smooth or slightly striate, dry or slightly greasy, not viscid when moist. Flesh in cap thin (up to 2.5 mm thick), in cap and stem rather firm and concolorous with surface; in centre of stem fibrous, pale yellowish. Smell and taste not distinct. Well-dried specimens dull ochre-orange or brownish ochre.

Spores [70/7/7] 6.5–10(–11.5) × 3.5–5(–5.5) μm, averages 7.5–9.3 × 3.7–4.7 μm, l/b 1.6–2.2(–2.4), ellipsoid-oblong, obovoid-oblong or cylindrical, sometimes pyriform but many (40–70%) clearly constricted in side-view and often in front-view too, with prominent rather large oblique apiculus (Figs. 31, 32). Basidia [40/6/6] (34–)36–58 × (5.5–)6–8 μm, l/b (4.6–)5.0–8.6, slenderly clavate, mostly 4-spored but in some collections a few 2- or 3-spored; sometimes mixed 2-, 3-, and 4-spored (then spores in part longer than 9 μm; Fig. 33). Pleuro- and cheilocystidia not seen. Trama of gills subregular, composed of subparallel to slightly interwoven hyphae with rather short cylindrical or somewhat inflated cells with obtuse ends, measuring [20/3/3] (32–)41–88 × (6–)8–18 μm, l/b (3.0–)3.4–10.7. Pileipellis a thin cutis, 20–40(–60) μm thick, composed of a few layers of colourless, mostly radially arranged, repent hyphae, sometimes very slightly gelatinized, with long cylindrical cells 2.5–6 μm broad; locally with scattered, narrow, ascending or erect ends sometimes constituting small fascicles (Fig. 34), downwards gradually passing in pileitrama. Hyphae close beneath pileipellis rather strongly interwoven, with short cylindrical or inflated cells 6–11 μm broad, in fresh fruit-bodies with bright yellow vacuolar pigment (a subpellis); pileitrama under this layer consisting of more regularly, radially disposed hyphae with rather short cylindrical cells 6–15 μm broad, with pale yellowish vacuolar pigment when fresh (Fig. 35). Stipitepellis a poorly differentiated dry cutis with long cylindrical cells 2.5–5 μm broad. Stipitetrama consisting of longitudinal subparallel hyphae 4–11.5 μm broad. Vascular hyphae not seen in trama. Clamps observed at base of basidia and at hyphae of pileipellis.

HABITAT.—In the Netherlands not common, mostly met with in moss-rich, unmanured grasslands on weakly acid, mesotrophic, sandy soil; also once in oak-scrub on sand. October-November.

COLLECTIONS EXAMINED.—THE NETHERLANDS: prov. Gelderland, Warnsveld, De Kop, 20 Oct. 1961, *E. Kits van Waveren s.n.* (L); prov. Noord-Holland, Aerdenhout, dunes of Amsterdam Water Supply, 6 Oct. 1961, *E. Kits van Waveren s.n.* (L); Island of Texel, De Koog, 29 Oct. 1971, *E. Arnolds 637* (L); prov. Zuid-Holland, Oostvoorne, Weevers' Duin, 6 Nov. 1970, *E. Arnolds 598* (L); prov. Noord-Brabant, Drunen, dike along Drongelens Kanaal, 22 Oct. 1970, *E. Arnolds 544* (L); 26 Oct. 1975, *E. Arnolds 3486* (WBS).

The preceding description is based on collections from the Netherlands. It agrees well with the diagnosis and the illustrations given by Orton (l.c.). I investigated also two of his collections (*Orton 1220* and *2987*, E), and found the same features, e.g.

spores 6.5–9.5×3.5–5 μm, many (40–50%) constricted in the middle. In literature this species has also been reported from Czechoslovakia (Svrček, 1962) and Chile (Singer, 1969). When studying collections from Central Europe, provisionally determined as *Hygrocybe marchii*, I came across a collection from Switzerland (Col de Julier, Sept. 1968, *M. Bon 80939*) which in my opinion is identical with *H. strangulatus*. The most important microscopical details are: Spores [10/1/1] 6.5–8×3.5–4 μm, l/b 1.6–2.0, ellipsoid-oblong but often clearly constricted in side-view (50–70%). Pileipellis a thin dry cutis c. 30 μm thick, with slender hyphae 1.5–4 μm wide.

In my opinion *H. strangulatus* is closely related to *H. marchii*, but in most cases it can be distinguished already in the field on account of the more slender habit, the less fragile flesh and the more hygrophanous cap (cf. Orton, 1960: 252). Microscopically it differs not only in having constricted spores but also in a thinner and drier pileipellis.

Some problems seem to exist about separating *H. strangulatus* from *H. miniatus* (Fr.) Fr. In my opinion the description and plate of *H. strangulatus* by Reid (1958) relate to *H. miniatus*. Orton communicated to me in a letter (27 Feb. 1976) that Dr. Watling and he '... feel that the spores given by Reid for *strangulatus* are not those of that species and that the plate much more likely represents *H. miniatus*'.

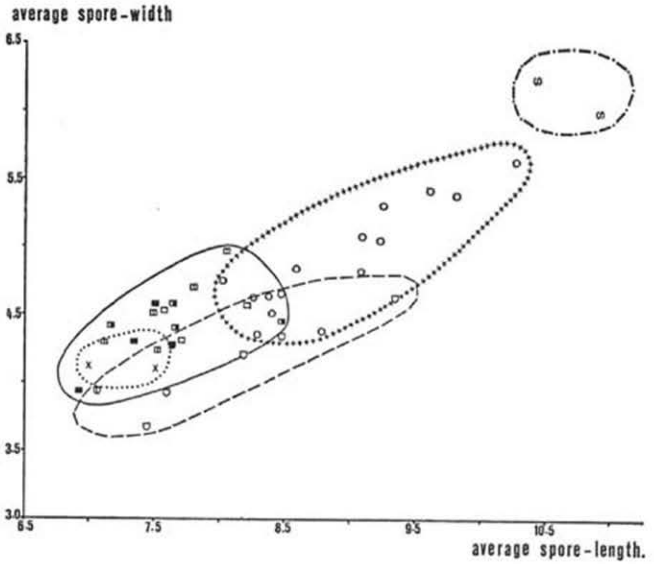
Two facts might have contributed to this misinterpretation: (i) Orton (l.c.) has described the cap of *H. strangulatus* being 'sometimes reflexed scurfy scaly round centre'; (ii) the spores of typical *H. miniatus* are often constricted in some views, but this feature has been rarely stated in descriptions, e.g. neither by Orton (l.c.) nor by Hesler & Smith (1963). In fact the cap of *H. strangulatus* is never really scaly but often covered with fine adpressed hairs. At most these constitute small irregularities, which give the cap a minutely roughened appearance under a hand-lens. Orton expressed the same opinion in the letter mentioned above. Close microscopical examinations indicate fundamental differences between the pileipellis in *H. strangulatus* and *H. miniatus*. In the latter the outermost tissue of the cap consists of hyphae with short, rather broad cells (5–15 μm), constricted near the septa, forming local fascicles of erect hyphae with broadly rounded clavate end cells (cf. Arnolds, 1974a: figs. 158, 159, 161; Hesler & Smith, 1963: fig. 8e).

Spores in *H. miniatus* are also different in shape: in side-view they are ellipsoid or ovoid and only rarely slightly constricted, but in front-view their shape is often constricted and typically widened towards the apiculus. This is shown in the drawing by Reid (l.c.: fig. 5) and also by Arnolds (1974a: fig. 152).

HYGROPHORUS SUBSTRANGULATUS P. D. Orton—Figs. 16–18

Hygrophorus substrangulatus P. D. Orton *in* Trans. Br. mycol. Soc. **43**: 269. 1960. — *Hygrocybe substrangulata* (P. D. Orton) P. D. Orton & R. Watling *in* Notes R. bot. Gdn Edinb. **29**: 131. 1969.

I have seen no fresh fruit-bodies of this species. Also no proof has been given till now of its occurrence in the Netherlands. So I refer to Orton (l.c.) for a macroscopic



□	*Hygrophorus marchii*	from the Netherlands
⊟	*Hygrophorus marchii*	from France and Switzerland
◨	*Hygrophorus marchii*	from Denmark
■	*Hygrophorus marchii*	from Great Britain
X	*Hygrophorus marchii* sensu Hesler & Smith	from the U.S.A.
O	*Hygrophorus phaeococcineus*	from the Netherlands
ᑌ	*Hygrophorus strangulatus*	from the Netherlands
⊎	*Hygrophorus strangulatus*	from Switzerland
●	*Hygrophorus strangulatus*	from Great Britain
S	*Hygrophorus substrangulatus*	from Great Britain

Fig. 36. Scatter diagram of average length and width of basidiospores of specimens examined of the *Hygrophorus marchii*-group.

description. Some microscopical details based on my investigation of two British collections are given below:

Spores [20/2/2] (8–)9–11.5(–12.5) × 4.5–6.5(–7.5) µm, averages 10.4–10.9 × 6.0–6.3 µm, l/b (1.5–)1.6–2.0, in side-view ellipsoid-oblong and rather frequently slightly constricted, in front-view often clearly constricted (Figs. 16–17). Basidia [20/2/2] (44–)47.5–63.5(–65.5) × (7.5–)8–10.5(–12) µm, l/b 5.3–7.1(–7.5), rather slenderly clavate, 4-spored (Fig. 18). Pleuro- and cheilocystidia not seen. Trama of gills subregular, consisting of subparallel hyphae with short cylindrical or inflated cells with rounded ends, c. 20–90(–140) × (6.5–)8.5–14 µm, l/b (2.3–) 2.6–10.7. Pileipellis difficult to study in detail, probably a thin dry cutis consisting of thin, repent, colourless hyphae with a few erect ends, 2.5–6(–7.5) µm wide. Pileitrama close beneath the pileipellis rather interwoven, consisting of weakly coloured hyphae 5–12 µm wide (a subpellis); downwards more regular with radial hyphae 7–17(–24) µm wide. Vascular hyphae present or not, irregularly flexuous, 3–6 µm wide. Well-dried specimens orange-ochre or dull-orange-brown (M. 5C6, D6).

COLLECTIONS EXAMINED.—GREAT BRITAIN: Studland, Dorset, 27 Oct. 1955, *P. Orton 477* (E; from type-locality); Loch an Eilean, Inverness-shire, 21 Aug. 1961, *P. Orton 2365* (WBS dupl.).

It is probably impossible to distinguish *H. substrangulatus* from *H. strangulatus* on macroscopic characters only. However, the spores of the first are significantly larger and more rarely and weaker constricted (Fig. 17). I only observed constriction in the face-view of a few spores in collection *Orton 477*. Spores are also significantly larger than those of *H. marchii* and *H. phaeococcineus*, as demonstrated in the scatter diagram of Figure 36.

Like *H. strangulatus*, *H. substrangulatus* can be easily mistaken for *H. miniatus* (Fr.) Fr. However, it seems to differ fundamentally in the structure of the pileipellis, which in the latter species is a trichoderm without narrow repent hyphae. The report by Barkman (1964: 22) of *H. cf. substrangulatus* in the Netherlands relates in fact to *H. miniatus*.

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EXPLANATION OF PLATE 20

Fig. a. *Hygrophorus strangulatus* (× 1, from *Arnolds 3486*). — Fig. b. *Hygrophorus phaeococcineus* (× 1, from *Arnolds 3710*). — Fig. c. *Hygrophorus marchii* (× 1, from *Arnolds 3278*). — Fig. d. *Hygrophorus helobius* (× 1, from *Arnolds 511*; see Persoonia **8**: 99. 1974). — All Figs. del. E. Arnolds.

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ELECTRON MICROSCOPIC STUDY OF CONIDIUM ONTOGENY IN CONIOTHYRIUM CUPRESSACEARUM (COELOMYCETES)

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(With Plates 30–31)

Coniothyrium cupressacearum (Morelet) Morelet, exhibiting annellated conidiogenous cells in light microscopy, was examined by transmission electron microscopy. Since the conidial wall is formed *de novo*, i.e. not continuous with a pre-existent layer of the conidiogenous cell wall, the conidiogenesis is clearly phialidic. After production of a number of conidia, a percurrent proliferation of the phialide collar occurs; this explains the annellated appearance. The annellide is not considered to be a special kind of conidiogenous cell but a variation of either the phialide or the aleuriophore.

Among the Fungi Imperfecti electron microscopic studies of Coelomycetes are scarce. Ultrastructural data like that obtained for many Hyphomycetes would be very useful, particularly in species with small sporogenous structures. Many uncertainties still exist as to the phialidic or annellidic nature of the conidiophores of such taxa, among them *Coniothyrium cupressacearum* (Morelet) Morelet. In 1970 this fungus, together with other species, was isolated from twig cankers of *Chamaecyparis lawsoniana* (Murr.) Parl. and *Cupressus sempervirens* L. in France and was first described as *Coniella cupressacearum* (Morelet, 1971a). Later, when subsequent examinations with a light microscope had shown that the conidiophores are annellated (Morelet, 1971b), *Coniella cupressacearum* was transferred to the genus *Coniothyrium* Corda.

By the concept of Sutton (1971) the genus *Coniothyrium* Corda (nom. conserv.) sensu stricto, with *C. palmarum* as lectotype, is indeed characterized by annellidic conidiogenous cells. According to Sutton this distinguishes *Coniothyrium* from *Microsphaeropsis* Höhn. (type species: *M. olivacea* Höhn.), which is characterized by phialides and should include many phialidic species such as the well-known *C. fuckelii* Sacc. It has now been established (Oláh & Reisinger, 1973) however that the annellide may result from two distinctly different processes:

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- Holoblastic development (succession of vegetative proliferations after thallic conidiogenesis).
- Enteroblastic development (succession of conidiogenous apices or primordia). The present authors think that there is enteroblastic development when the primordium wall is not continuous with a pre-existent layer of the conidiogenous cell (Reisinger, 1972; Mangenot & Reisinger, 1976).

It is therefore of interest to investigate the annellides of *C. cupressacearum* by electron microscopy in order to establish the fundamental mechanism of its conidiogenesis. As far as we know, the only ultrastructural data on the *Coniothyrium*-group published so far deal with phialidic species such as *C. fuckelii* and *Microsphaeropsis olivacea* (Jones, 1976).

In accordance with previously established principles (Reisinger, 1972; Reisinger & Mangenot, 1973; Mangenot & Reisinger, 1976), in the study of conidiogenesis we have separated conidiophore development from conidial ontogeny. In conidial ontogeny we note three distinct steps: (i) primordium initiation, (ii) conidium maturation, and (iii) conidium liberation. These steps will be examined separately.

MATERIAL AND METHODS

The strain used for our study was the type culture of *C. cupressacearum* isolated in October 1970 from a twig canker of *Chamaecyparis lawsoniana* in the Southwest of France (Morelet, 1971a) and deposited in Baarn under the number *CBS 874.72*. The fungus was cultured in daylight on beer wort (18° Balling) with 2% agar at room temperature (c. 20° C.) for 24 days, by which time it had reached a diameter of 40 mm. Pycnidia of different ages were removed from the plates and fixed in 2% osmium tetroxide at pH 7.4 or in 2% unbuffered potassium permanganate for 2 h. at room temperature. After they had been dehydrated in an ethanol gradient and included in Epon, serial sections were made with a diamond knife. Sections were contrasted with lead citrate (Reynolds, 1963) or else with TCH (thiocarbohydrazide) by the method proposed by Thiéry (1967) for polysaccharide differentiation.

RESULTS

Conidial ontogeny.

PRIMORDIUM INITIATION.—The conidiogenous structures inside pycnidia are closely entangled with other fertile or sterile cells. They are either long and phialide-like or short obconical (Pl. 31 fig. 7). In mature pycnidia the apex of the conidiogenous cells is usually provided with an opening surrounded by a typical thickening, well known in subendogenous phialides (Pl. 30 figs. 1–5, Pl. 31 figs. 6, 7).

Successive conidia are formed by extrusion through the collar opening. Each primordium is separated from the preceding conidium by a perforated wall (Pl. 30 fig. 1) structurally analogous to ascomycetous walls but without Woronin bodies. The wall is made up of two layers originating in the lateral wall and separated by a cleavage zone; the lower layer later becomes the fundamental layer of the next primordium (Pl. 30 figs. 1, 3, 4). The primordium wall originates in the zone below the annular thickening of the collar; since it is not continuous with a pre-existing layer (Reisinger, 1972) it is formed *de novo*. The detection of polysaccharides by Thiéry's TCH technique is well suited for the study of this zone in which neither lead citrate (Pl. 30 fig. 1) nor permanganate (Reisinger, unpublished data) gives enough contrast. The same was observed earlier in phialides of *Phialophora richardsiae* (Oláh & Reisinger, 1974). Provided the section is favourably oriented TCH coloration will reveal a stratification in the annular thickening of the collar. These layers seem to result from deposits left in the course of successive conidium production. Lead citrate fails to give enough contrast to the young wall of the primordium (Pl. 30 fig. 1) but TCH provides good differentiation between the collar thickening and the newly formed wall of the new primordium (Pl. 30 fig. 2). The plasmalemma in the primordium and the upper part of the phialide is deeply corrugated, thus revealing strong physiological activity in these zones.

CONIDIUM MATURATION.—The wall of the young primordium thickens with age but exhibits no differentiation between the layers. In young pycnidia, conidia are hyaline even after secession and their outer surface is covered with a loose granular structure. In accordance with our terminology (Reisinger, 1972; Mangenot & Reisinger, 1976) we can distinguish an A-layer and a B-layer (Pl. 31 fig. 11). During maturation dark pigments are deposited in the wall by a process described by Reisinger & al. (1977) and in this way delimit the two sublayers B_1 and B_2 (Pl. 31 fig. 8). Such a development in the conidial walls is consistent with that of haplothecate conidia (Mangenot & Reisinger ,1976). Some pictures suggest that the primary wall participates in the formation of the mucilage surrounding the conidia (Pl. 30 figs. 2, 4, 5).

CONIDIUM LIBERATION.—The successive steps in conidium liberation can be reconstructed from Figs. 1, 3, 4, 5, 2 and 6 on Plates 30 and 31. The wall delimiting the young conidium from the next primordium is progressively lysed in the cleavage zone (Pl. 30 figs. 4, 5). Conidia remain tied together by residual products of lysis remaining between the layers of the wall (Pl. 30 fig. 2, Pl. 31 fig. 6).

Development of the conidiogenous cell.

In old pycnidia long annellide-like conidiogenous elements were seen, which confirms previous observations with light microscopy. A thorough ultrastructural examination of these structures led us to interpret them as the result of a series of successive proliferations. The whole structure is made up of encased phialide collars. We assume that each stage functions for some time as a phialide producing a number of conidia; this might account for the thickness of the collar deposit (Pl. 31 fig. 9).

Mucus.

Different contrasting techniques reveal slight variations in the appearance of the mucus in the pycnidial cavity. With lead citrate its granules seem to be arranged in lines, giving them a fibrillar aspect. TCH shows a more random disposition of the strongly reactive granules, except in zones surrounding primordia (Pl. 30 figs. 2, 4, 5). This led us to the hypothesis that the mucus might originate from the primary wall.

In old pycnidia the cells in the pycnidial cavity degenerate. The autolysis causing the degeneration affects even the cell wall. The cell wall ruptures and the altered cell contents leak out (Pl. 31 fig. 10). A similar process was seen in lysis of *Coprinus* carpophores (Sokolski & al., 1976).

Conclusions

Ultramicroscopic examination of the steps of conidium ontogeny in *C. cupressacearum* reveals that its spores are phialoconidia with all the production mechanisms judged to be typical of this kind of propagulum (Reisinger, 1972; Reisinger & Mangenot, 1973; Mangenot & Reisinger, 1976; Kiffer & al., 1971). The nature of its conidiogenesis places this species in the group of phialidic fungi with conidial heads as recently defined by Roquebert (1976). It should be emphasized that the first part of the primordial conidial wall is formed by the lower layer of the septum that separates the previous conidium from the newly developing conidium.

Initially this septum is perforated and similar to the hyphal septa but it lacks the Woronin bodies associated with vegetative septa. The photographs obtained to date do not reveal the mechanism that eventually closes the septal perforation.

It is our conclusion that the functioning of the phialide of *C. cupressacearum* is identical in all respects to that of *Phialophora richardsiae* (Oláh & Reisinger, 1974). Except in minor details, it is also similar to the conidiogenesis in *Doratomyces purpureofuscus* (Kiffer & al., 1971), which possesses annellides of the first type, viz. the type with enteroblastic development.

The other type of annellide, that with holoblastic development, results from a quite different process, the best known example of which is *Monotosporella* (=*Acrogenospora*) *sphaerocephala* (Reisinger, 1972). In this fungus the annellated appearance of the conidiophore results from the emission of proliferations after the formation of each of the blown-out conidia (Hammill, 1972a; Oláh & Reisinger, 1973; Mangenot & Reisinger, 1976; Reisinger & al., 1977).

Separate analysis of conidiophore development and conidial ontogeny reveals the annellide-like structures of *C. cupressacearum* as merely vegetative proliferations whose apices resume conidiogenous activity for varying periods of time.

Such a mode of evolution of conidiophores by successive proliferations is not rare among fungi, especially phialidic species (Hughes, 1971). In Coelomycetes it was described by Morgan-Jones & al. (1972).

We consider the conidia of *C. cupressacearum* to be typical phialoconidia. They are characterized by a primordium which is surrounded by a newly formed wall that is not continuous with any of the pre-existing layers of the phialide wall. They are different from thalloconidia (sensu Reisinger & Mangenot, 1973) whose primordium originates from the usual mechanisms of hyphal growth and whose walls are continuous with a pre-existing layer of the conidiogenous cell, either internally or externally.

Because of its multilayered aspect the thickening around the phialide neck seems to be produced by successive deposits of wall material during conidiogenesis. This material may exist in phialides however before conidiogenesis (Jones, 1976). Its existence seems to be very widespread among phialidic fungi, including species with monoconidial phialides (Gams, 1973), the few Coelomycetes so far investigated (Brewer & Boerema, 1965; Sutton & Sandhu, 1969; Boerema & Bollen, 1975; Jones, 1976), and many Hyphomycetes. The thickening has even been compared to the denticle plug of 'Radulasporae' (Gams, 1973) and to the apical swelling of the ascus (Delespine & Chadefaud, 1960; Chadefaud, 1974). Therefore even if any deposition of wall material occurs it cannot entirely explain the swelling of the phialide necks.

As already stated, electron microscopic studies of Coelomycetes are scarce (Brewer & Boerema, 1965; Sutton & Sandhu, 1969; Hammill, 1972b; Boerema & Bollen, 1975; Jones, 1976).

Sutton & Sandhu examined four species, among them a *Cryptosporiopsis*, and concluded that these fungi possess annellides. Since then a closer examination of this type of conidiogenesis has led to a distinction between two types of annellides. The first is linked to phialidic conidiogenesis, the second produces aleurioconidia with percurrent proliferations (Reisinger, 1972; Hammill, 1972a, 1974, 1977). Of the four species studied by Sutton & Sandhu *Cryptosporiopsis* species and *Phoma fumosa* belong to the first type (see Jones, 1976) and the two *Melanconium* species to the second type. According to data by Hammill (1972b) *Stegonosporium pyriforme* produces its conidia by the phialidic process. All the species studied by Jones (1976) are phialidic. Boerema & Bollen (1975) examined a number of species of *Phoma* and *Ascochyta*, and concluded that *Phoma* is phialidic while *Ascochyta* is annellidic. In *Phoma* all the conidia, including the first one, are enteroblastic; the collar thickening is a remnant of the initial thick papilla of the phialide and is not increased in width by the deposition of new material during conidiogenesis. In *Ascochyta*, in addition to the presence of the annellated collar typical of annellides, the first conidium is holoblastic but subsequent conidia could not be shown to be truly holoblastic. Boerema & Bollen used these and other characteristics to establish a clear-cut distinction between the two genera.

However, if the grouping of *Ascochyta*-type annellides and phialides together is accepted then the limited data on the ultrastructure of conidiogenesis in Coelomycetes gathered to date, reveal only two types of conidia: phialospores (common) and aleuria (rarer). The existence of percurrent proliferations, in some instances in both groups, explains the annellidic aspect seen in light microscopy.

Contrary to the opinion of Jones (1976) we think that phialo- and annelloconidiogenesis (first type) are truly similar and that a distinction between the two kinds of conidiogenous cells is only practical in value. Gams (personal communication) also thinks that the above distinction between phialidic *Phoma* and annellidic *Ascochyta* is 'very useful, but less fundamental than Boerema & Bollen suggest'. Hammill (1974, 1977) seems to share this opinion, stating that the distinction between phialides and annellides is tenuous; both types produce enteroblastic conidia (except in that the first conidium of annellides could be holoblastic, i.e. surrounded by the wall of the annellide apex). In both cases the lower part of the separating septum becomes part of the wall of the next conidium so that in the end a continuum rather than a sharp distinction might exist between phialide and annellide.

The purpose of our work was to closely examine the conidiogenous cells of *C. cupressacearum*; when seen with the light microscope these appear to be annellides like in the type species of *Coniothyrium*. Electron microscopy shows that these cells are true phialides with percurrent proliferations. A study of *C. palmarum*, type species of *Coniothyrium*, is needed to permit conclusions on the systematic position of this genus and related genera.

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RÉSUMÉ

Coniothyrium cupressacearum (Morelet) Morelet montre en microscopie photonique des cellules conidiogènes annelées. Il a été examiné en microscopie électronique à transmission. La conidiogenèse est clairement phialidique, la paroi conidienne est néoformée, c'est-à-dire qu'elle n'est pas en continuité avec une couche préexistante de la paroi de la cellule sporogène. Après production d'un certain nombre de conidies, le col de la phialide repousse de façon percurrente, ce qui explique l'aspect annelé vu au microscope photonique. L'annélide n'est pas considérée comme une cellule sporogène spéciale mais comme une variante, soit de la phialide, soit de l'aleuriophore.

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EXPLANATION OF PLATES 30–31

PLATE 30

Figs. 1–5. *Coniothyrium cupressacearum*, various steps in conidium formation, maturation, and secession. Mucus seems to originate in part from the outer layers of the young conidial walls (Figs. 4, 5). (Fig. 1, stained with lead citrate; Figs. 2–5, stained with TCH).

PLATE 31

Figs. 6–11. *Coniothyrium cupressacearum*. — 6. Conidium secession (TCH). — 7. Short obconical sporogenous cell (TCH). — 8. Mature conidium, A and $B(=B_1+B_2)$ layers (lead citrate). — 9. Successive encased collars of a phialide (TCH). — 10. Lysis of an aged cell, probably contributing to the production of mucus (TCH). — 11. Maturing conidia (TCH).

PERSOONIA
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BOOKS RECEIVED BY THE RIJKSHERBARIUM LIBRARY

J. BLUM, *Les lactaires.* (Etudes mycologiques **3**, Lechevalier, Paris 1976). Pp. 371, 16 col. pls., 94 text-figs. Price: fr. 90.—.

This booklet gives an introduction to the study of the genus *Lactarius* and a survey of its European species. Keys are presented; variability and relationships of the species are amply discussed.

R. KÜHNER & H. ROMAGNESI, *Compléments à la "Flore analytique"* (Reprint edition in Bibliotheca mycologica **56**, J. Cramer, Vaduz 1977). Pp. 484, 188 text-figs., 1 pl. Price: DM 100.—.

A reimpression of R. Kühner & H. Romagnesi's supplements to their widely used 'Flore analytique des champignons supérieurs' of 1953, published between 1954 and 1958 in various journals. The supplements contain many original and extensive, often illustrated descriptions of new and insufficiently known taxa of European Agaricales.

C. A. J. A. OUDEMANS. *Contributions à la flore mycologique des Pays-Bas I–XX* (Reprint edition in Bibliotheca mycologica **54**, J. Cramer, Vaduz 1977). Pp. 1060, illustrated. Price: DM 300.—.

A reprint edition of a series of papers published between 1872 and 1904 (the first decade in Dutch, together 217 pages, the second decade in French), forming a major contribution to the knowledge of the higher and lower fungi then known to occur in the Netherlands. Many of Oudemans' new species are described in these papers.

W. UELLNER, *Fungorum libri bibliothecae Joachim Schliemann* (J. Cramer, Vaduz 1976). Pp. 287, 34 full-page reproductions of title-pages. Price: DM 60.—.

A catalogue of mycological books, journals and reprints in the library of J. Schliemann, Hamburg, with references to reviews and bibliographical literature.

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NOTES AND BRIEF ARTICLES

MYCENA GALERICULATA—USUALLY 2-SPORED?

R. A. Maas Geesteranus

Oegstgeest

Mycena galericulata (Scop. ex Fr.) S. F. Gray is a common agaric, widely distributed in Europe and readily recognized. Whether this also applies to extra-European areas is here left out of consideration, while the actual investigation is concerned only with the situation in the Netherlands.

As far as I have been able to check, the general opinion in Europe has been and still is that *M. galericulata* occurs predominantly with 2-spored basidia. A few references may be cited to substantiate this statement; some care had to be taken in consulting those authors who regarded *M. galericulata* and *M. rugosa* Fr. (now considered to represent one and the same species) as distinct.

Hennig (1958: 108): 'Basidien zweisporig'; Horak (1968: 391): 'Basidien 2sporig (selten 4sporig)'; Konrad & Maublanc (1948: 311): '... le plus souvent bisporique...'; Kühner (1938: 324): '[forme tétrasporique] Octobre-Décembre ... aux environs de Paris..., où il semble moins commun que le *M. galericulata* bisporique'; (1938: 326): '[forme bisporique] Très commun ... de mars à décembre...'; Kühner & Romagnesi (1953: 108): '... race bisporique, la plus commune...'; Lange (1936: 47): 'Basidia 2-spored'; Oort (1928: 241): 'Basidiën 2-sporig' (23 collections); he (p. 230) also recorded a single, 4-spored collection of what he took to be *M. rugosa*, but he felt uncertain about his own identification. His description does not suggest *M. galericulata*, and this find seems best disregarded. Patouillard (1885: 145) proves to be an exception in European literature in that he is the only author to have illustrated 4-spored basidia: '... hyménium grossi montrant des basides à 4 stérigmates...'; Pearson (1955: 56–57); '... basidia usually 2-spored ...'; Rea (1922: 383): 'Basidia generally with 2-sterigmata only'; alongside of *M. galericulata* he also recognized a *M. rugosa* with 2–4-spored basidia. Ricken (1915: 439), too, distinguished *M. galericulata* and *M. rugosa*, the former 2-spored and exceedingly common, the latter 4-spored and rather rare. Viennot-Bourgin (1959: 79): 'Basides typiquement à 2 spores'; Wakefield & Dennis (1950: 89): 'The basidia are almost always two-spored'.

Some of the less sophisticated questions that may be asked are (i) whether it is true that the 2-spored forms are more numerous than the 4-spored, and if so (ii) in what ratio they occur. No doubt questions of such or a similar nature have been posed in the past, but I am unaware of a definite answer having been published. The following investigation, carried out on herbarium material, confirms to some extent the general opinion, partially answers the second question and, above all, seems to offer interesting prospects for experimentalists.

For the present examination I assembled 72 collections from the Netherlands and one drawing showing microscopic details. Of the former 19 proved unsuitable for various reasons (the month of collecting was not stated; one collection belonged to a different genus; some collections proved to have been misidentified; others were immature or their basidia lacked sterigmata; etc.). The data derived from the drawing and the remaining 53 collections are presented in Fig. 1, in which the collections with 2-spored basidia are indicated by the symbol o, those with 4-spored basidia by ●.

As can be seen at a glance, all collections of *Mycena galericulata* gathered from May to September (V–IX) are of the 2-spored form. Apparently no basidiomes of *M. galericulata* were collected in June. October (X) is the month when a few collections of the 4-spored form make their appearance for the first time, while the following two months (XI and XII) show a considerable numerical increase of the 4-spored form. In December there usually occur some days of frost which put an end to most agarics. In order to express more clearly the ratio of the numbers of the 2-spored and the 4-spored forms, the following graph (Fig. 2) is presented, in which rather than the collections being indicated by their actual numbers, their relative proportions are expressed by percentages, correlated with the month of collecting.

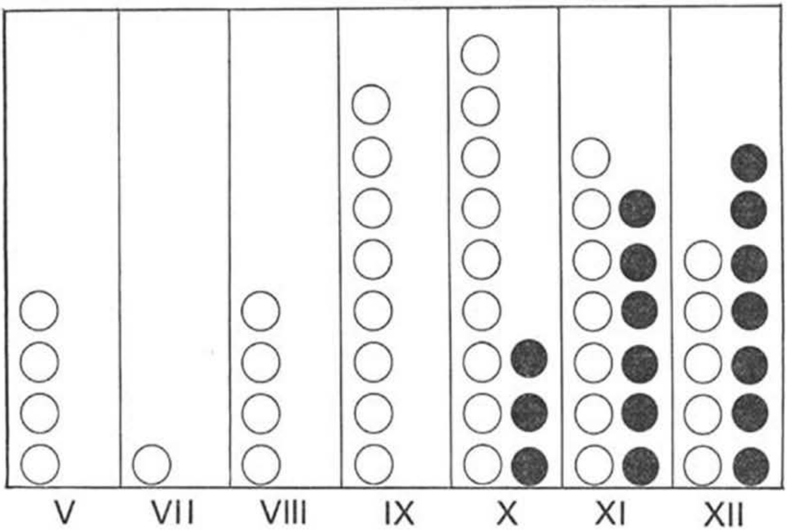

Fig. 1. *Mycena galericulata*. Collections arranged according to the month of collecting; the symbol o denoting a collection with 2-spored basidia ● denoting one with 4-spored basidia.

If, as I am inclined to assume, the lower temperatures during the last months of the year have something to do with the conspicuous decline of the 2-spored form (and the corresponding increase of the 4-spored form), it may well be pointed out that the curves as drawn have but an approximative value. The data used have been derived from collections which span a period of more than 110 years, the oldest collection being from 1864. It is beyond doubt that the temperatures of the fungus seasons in those years must have varied a great deal. Perhaps even more important than the influence of the macroclimate ought to be considered that of the microclimate. It is not known, however, at what stage in its development the temperature may cause *Mycena galericulata* to produce either 2-spored or 4-spored basidia. General information, therefore, on the fluctuations of the temperature as may be provided by a meteorological institute is not likely to be of great help. In order to understand the processes that determine the nature of the phenomenon discussed above, experiments will be needed under strict control of all environmental factors.

Thus far, the 2- and 4-spored basidiomes have been regarded as simple forms of the taxonomic entity *Mycena galericulata*, but there is yet another possibility which requires serious attention, and which suggests that the basidiomes referred to belong to genetically different taxa.

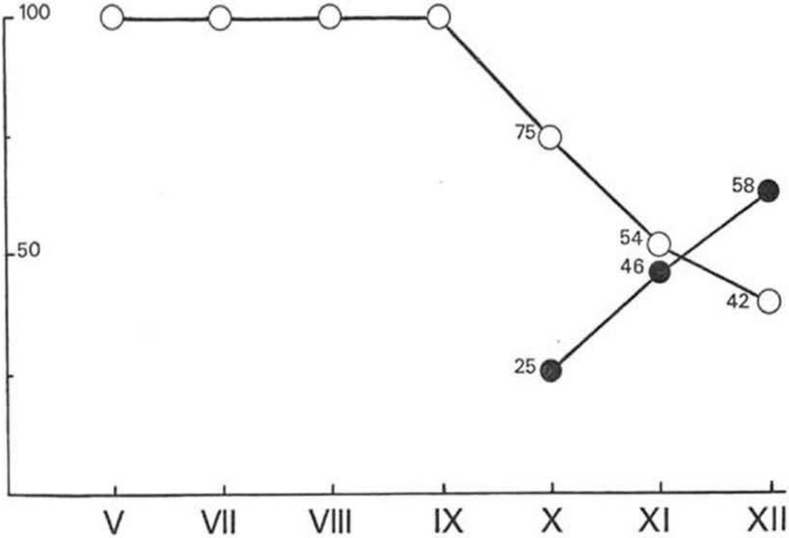

Fig. 2. *Mycena galericulata*. Graph illustrating the different course of the percentages of the collections with 2- and 4-spored basidia during the fungus season.

Apart from the collections preserved in the Rijksherbarium (also housing the collections of the Royal Dutch Botanical Society, the Dutch Mycological Society, and Herb. Oudemans), material has been examined from Centraalbureau voor Schimmelcultures (CBS), Biologisch Station Dr. W. Beyerinck, Wijster (WBS), Dr. H. A. van der Aa (Baarn), Mr. P. B. Jansen (Breda), and Dr. E. Kits van Waveren (Amsterdam). To all these I tender my best thanks.

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PROBLEMS AROUND A NEW MUCRONELLA

R. A. Maas Geesteranus

Oegstgeest

Mucronella styriaca Maas G., *spec. nov.*[1]

Habitu coloreque *Mucronellae flavae* Corner similis, ab hac tamen diversa subiculo manifesto, proventu caespitoso, sterigmatibus longioribus, sporis majoribus, cystidiis hymenialibus. Holotypus in GZU, fragmentum typi in L.

Fungus resembling by its habit and colour *Mucronella flava* Corner, from which it differs in possessing a well-developed subiculum, caespitose growth, longer sterigmata, larger spores, and hymenial cystidia.

Corner (1953: 356) mentioned the presence of abundant crystals in the tissue and on the surface of the stem of *M. flava*. There are none in *M. styriaca*.

Basidiome consisting of spines hanging down from a subiculum. Subiculum very sparse or more or less densely arachnoid to almost pulverulent-tomentose, yellowish white, producing stipitate spines. Stipe (dried) up to about 1 mm long, 0.1 mm wide, cylindrical, minutely powdered, whitish to corneous-translucent. Spines (dried) up to 2 mm long, up to 0.2 mm wide, pointing downwards, caespitose, more rarely growing separately, simple or coalesced or furcate at the base, subulate, with acute apex, yellowish white to pale straw yellow (fresh: vitellin with paler tips).

Context of the spines monomitic, made up of generative hyphae only. Subicular hyphae up to 9 μm wide, moderately thick-walled, with clamp-connections. Generative hyphae 3.6–10 μm wide, thin-walled, with clamp-connections, branched, anastomosing, somewhat inflating, firmly coherent, in the stipe becoming narrower towards the sides and producing hair-like excrescences (Fig. 1). Basidia 20–25 × 6.5–7 μm, clavate, with 4 sterigmata up to 7 μm long, with basal clamp (Fig. 2). Spores 5.5–7.3 × 3.8–4.3 μm, pip-shaped and often slightly triangular, smooth, colourless, without oil-drops, pale blue amyloid. Cystidia of hymenial origin, thin-walled, somewhat narrower than the basidia and little or not projecting (Fig. 2), contrasting with the latter in that their contents are stained a different shade of red in Congo Red, not becoming stained by sulfo-benzaldehyde.

Holotype: '[Österreich,] Ostalpen, Koralpe, Steiermark: Garanas bei Schwanberg, nahe der Pauritsch Kapelle im Wald, ca. 640 m', 26 Sept. 1976, *S. Michelitsch*, apparently growing on very rotten wood (GZU; fragment of holotype in L).

In trying to identify the present fungus, Corner's keys (1970) left no other choice but to regard the species as a member of *Mucronella*, although this assignment raised some questions, the most important one being that this genus was reputed normally to have no cystidia. These questions, as so often happens, proved to be tied to others,

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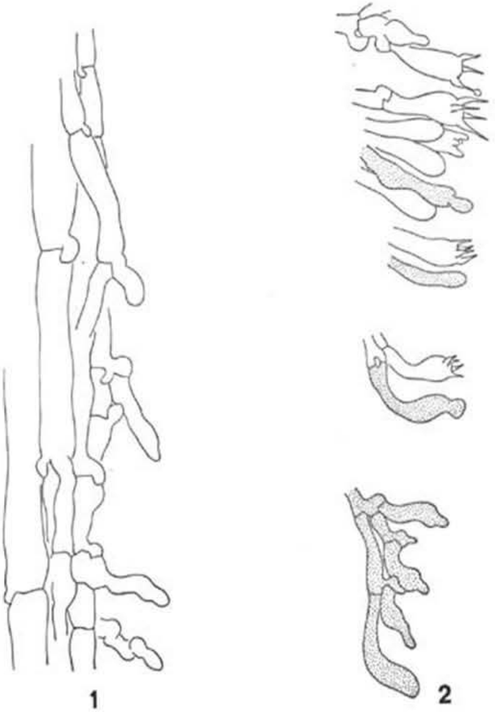
[1] Etymology: *styriaca*, derived from Styria, Steiermark.



Figs. 1–2. *Mucronella styriaca* (holotype). — 1. Outer part of the stipe, showing hair-like excrescences. — 2. Detail of the hymenium with basidia, cystidia, and sterile cells near the tip of the spine. (Both Figs., × 700.)

of which, I am sure, Donk must have been aware. He may have considered it inappropriate to go into greater detail at the time (1971), but the matter seems to me to be sufficiently important to be outlined on the following pages.

Corner (1950: 95) said of some of the species of *Mucronella* that 'their structure is the same as in the truly Clavarioid fruit-bodies of Ceratellopsis, which differ in growing upward instead of downward as those of Mucronella'. It was too early, as yet, to formulate a more definite statement.

Donk (1964: 252) placed *Mucronella* with the Clavariaceae, but there is a telltale line on p. 270 indicating that he obviously had thought of incorporating the genus into the Hericiaceae, but refrained from doing so because *Mucronella* lacked a 'conspicuous gloeocystidial system ... taken to be of primary importance [in characterizing the Hericiaceae]'.

At this juncture it seems appropriate to reproduce Donk's (1964: 233) definition of gloeocystidia: 'Gloeocystidia are usually more or less inflated, often ventricose or even vesicular bodies clearly differentiated from the hyphae from which they originate not only in their contents but also in diameter and shape'. He admitted, however, that gloeocystidia may also be hypha-like, with gloeocystidia-like terminations in the hymenium. With this emendation he introduced an element that would cause him to deviate from his original concepts.

In his card index I found that Donk evidently had changed his mind later on and had entered not only *Mucronella* but also *Amylodontia parmastii* Nikol. among the genera of the Hericiaceae. The Latin description of the latter species (Nikolajeva, 1967: 238)—the specific epithet of which I would have preferred to spell *parmastoi*—mentions the rare presence of cystidia. The true nature of these organs greatly puzzled Nikolajeva, as is borne out by the sentence: 'Species ... *Hericio fragili* (Fr.) Nikol. [=*Dentipellis fragilis* (Pers. ex Fr.) Donk] simillima est, sed gloeocystidiis nullis (nunquam bene evolutis) ... differt'.

The two examples mentioned above show that Donk no longer felt any scruples in incorporating into the Hericiaceae (a family he had proposed himself) genera which lacked an essential familial character—the gloeocystidial system. But there is more.

Corner (1970: 171–173) similarly placed *Mucronella* in the Hericiaceae, stating of the genus that 'there are no gloeocystidia or well-formed cystidia'. The latter part clearly refers to a description given by Malençon but is open to comment. Malençon (1958: 321), in redescribing the species Corner was to rename *Mucronella bresadolae* (Quél.) Corner (1970: 172), found the species to possess 'cystidioles ... tantôt rares ou même absentes, tantôt très nombreuses, d'origine hyménienne et répondant à des basides stériles étirées en poils étroits, simples ... demeurant inclus entre les basides ou dépassant l'hyménium de 10–20 μ'.

Firstly, even if it is true that the cystidia in *M. bresadolae* are very slender indeed and may with some imagination be compared to sterile basidia, this certainly does not apply in the case of *M. styriaca*. Secondly, in her description of *Amylodontia parmastii* Nikolajeva observed that the hyphae in the apex of the spines were sometimes filled with yellow matter and terminated with swollen tips. Thirdly, Corner (1970: 170) in a figure drawn after Siberian material (Parmasto 12993) showed the hymenial details of a fungus which, although possessing gloeocystidia, differed from *Dentipratulum bialoviesense* as described by Domański (1965: 7) in lacking a gloeoplerous[2] system, of which in general the gloeocystidia constitute the terminal ends.

The above three points, in connection with the aspect of the cystidia of *M. styriaca* as shown in Fig. 2, strengthen my opinion that in some of their characters the smaller-sized Hericiaceae display a truly remarkable series of smoothly graded steps: well-developed gloeoplerous hyphae terminating in gloeocystidia (*Dentipellis* Donk, *Dentipratulum* Domański); no gloeoplerous hyphae but unambiguous gloeocystidia

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[2] The term 'gloeoplerous hyphae' was coined by Donk (1971: 18).

present (*Dentipratulum* sp.: Parmasto 12993); gloeocystidia-like hyphae present among the basidia (*Mucronella styriaca*, *Amylodontia* Nikol.); basidia mixed with sterile organs which do not resemble gloeocystidia and which are numerous or rare or may be absent altogether (*Mucronella bresadolae*); hymenium with no cystidia at all (*Mucronella* Fr.).

There are yet other series in this group, although they may prove to be of lesser importance, as e.g. basidiome made up of a single spine (*Mucronella*, Corner, 1950: 95)—basidiome consisting of clustered or branched spines (*M. styriaca*); without a subiculum (*Dentipratulum*) — with a thin, arachnoid subiculum (some species of *Mucronella*)—with a dense, almost tomentose subiculum (*M. styriaca*)—with a thin, woolly subiculum and a long rooting base penetrating the substratum (*M. bresadolae*) —consisting of a membranous basal layer (*Dentipellis*, *Amylodontia*).

Overlooking these multiple series, I am under the steadily growing impression that not all of the genera so far mentioned constitute separate taxa. *Dentipratulum*, by way of example, could easily be merged with *Dentipellis*, from which it merely differs in lacking a membranous basal layer, a feature that in my eyes is of specific rather than generic significance. Further considerations, however, seem to make it inadvisable as yet to take this step, since it eventually would lead to all three genera —*Amylodontia*, *Dentipellis*, and *Dentipratulum*—becoming united with *Mucronella*. Keeping in mind moreover (1) that *Mucronella bresadolae* with its long rooting base 'may well be regarded as an intermediate' (Corner, 1970: 173) and (2) how little it would actually take to amalgamate a greatly enlarged *Mucronella* (with correspondingly vaguer generic limits) with *Hericium* Pers. ex S. F. Gray, it becomes clear that here looms the other extreme, and certainly one which is equally unsatisfactory.

Acknowledgement is made to the Director of the Rijksherbarium for providing working facilities. I am indebted to Prof. Dr. J. Poelt, Graz, for sending material that incited the reinvestigation of a problem in the Hericiaceae above the level of describing a new species.

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A NEW SPECIES OF MARASMIELLUS FROM THE NETHERLANDS

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Until recently the mycoflora of the West Frisian Islands has been rather neglected. In the last few years, however, members of both the Rijksherbarium and the Netherlands' Mycological Society (N.M.V.) have been collecting more frequently on these islands. The results of their fieldtrips are promising for the future as many interesting and rare fungi have been found.

In a previous paper (Noordeloos, 1975) I described a rare species of the genus *Marasmiellus* Murr., viz. *M. caespitosus* (Pat.) Sing. from the Island of Texel[1]. I now want to introduce, from the same island, another member of the same genus.

The collection on which the following description is based was sent to the Rijksherbarium by Dr. & Mrs. F. Tjallingii. It appeared to represent a species of *Marasmiellus* with remarkably distant lamellae with conspicuously thickened edges. In addition, the microscopic characters of this species are in many respects so different from those of the other members of the genus, that I do not hesitate to propose the following as a new species.

Marasmiellus pachycraspedum Noordeloos, *spec. nov.*

Figs. 1–4

Pileus 5–12 mm latus, convexus, opacus, coactus, humidus brunneolus, siccus centro fuscus, margine bubalinus rufo-tinctusque. Lamellae 16–20 (lamellulae 1–2), adnatae, crassiusculae, ventricosae, acie insigniter crassae, concolores, siccae paulum discolores. Stipes 10 × 1.0–1.5 mm, insititius, aequalis, fuscus, dense sordide albo-floccosus. Odore saporeque ignotis, probabiliter inconspicuis. Sporae (5.9–)6.5–8.0 × 4.5–5.5 μm, in cumulo albae, late ellipsoideae, tenuitunicatae, hyalinae, glabrae, inamyloideae. Cheilocystidia 60–120 × 10–18 μm, numerosa, gracilia, clavata, basi fibulata, tenuitunicata, pallide brunneo-incrustata. Pleurocystidia nulla. Pileipellis filamentosa, radialis, 'structura Rameales' nominatur nulla vel valde infirma. Stipitis pili coralloidei, incolores vel brunnei, 4–8(–10) μm lati. Carpophorum elementis amyloideis ac metachromaticis carens. Ad terram inter muscos. Typus: 'The Netherlands, prov. Noord-Holland, Isl. of Texel, the 'Slufter', 29 Oct. 1976, *F. Tjallingii & G. Tjallingii-Beukers*' (L).

Etymology: παχύς, thick; κράσπεδον, edge.

Pileus 5–12 mm broad, convex, opaque, felted, brownish when moist, drying buff with russet tinge but centre remaining darker. Lamellae 16–20 with 1–2 lamellulae

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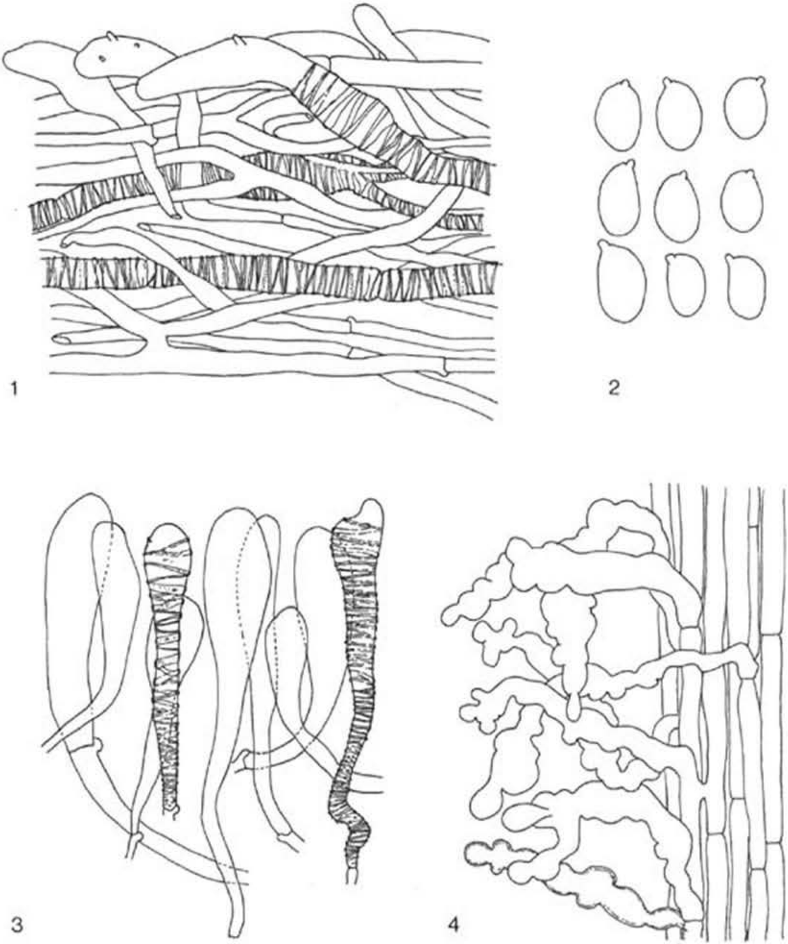
[1] This species has recently been found to occur also on another of the West Frisian Islands, viz. on the Island of Schiermonnikoog.

between each pair, narrowly adnate, thickish, ventricose with remarkably thick, (when dry) slightly darker edge. Stipe 10 × 1.0–1.5 mm, equal, dark with dense, sordid-white floccose covering, instititious. Smell and taste not noted (probably inconspicuous). Spore print white.

Spores (5.9–)6.5–8.0 × 4.5–5.5 μm, broadly ellipsoid, thin-walled, hyaline, glabrous, inamyloid. Basidia 4-spored, clamped, mature ones very scarce in dried



Figs. 1–4. *Marasmiellus pachycraspedum*. — 1. Pileipellis. — 2. Spores. — 3. Cheilocystidia. — 4. Stipitepellis. (All Figs. × 1000.)

specimens. Cheilocystidia 60–120 × 10–18 μm, numerous, slender, clavate, clamped, thin-walled, sometimes finely to heavily encrusted with brown substance. Pleurocystidia none. Trama of lamellae regular, hyphae cylindric to inflated, clamped, with brown, mainly membranal, but sometimes also encrusting pigment. Pileipellis filamentous, without a true Rameales-structure, hyphae radially arranged, 4–10 μm wide, glabrous or encrusted with brown substance, with scattered subclavate, sometimes encrusted, ascending terminal ends of thin-walled tramal hyphae, rarely with one or more pointed appendices. Pileitrama regular, consisting of radially arranged, 5–12(–20) μm wide, inflated hyphae, often with brown, membranal or encrusting pigment; pigmentation most abundant just above hymenium. Stipitepellis with densely clustered thin- or slightly thick-walled 4–8(–10) μm wide, colourless or brownish coralloid hairs. Stipitecortex composed of parallel, cylindric, sometimes anastomosing, thin-walled, pale brown, sometimes encrusted hyphae.

No part of carpophore with any (pseudo-)amyloid (in Melzer's reagent) or metachromatic (in cresyl-blue) elements.

HABITAT.—Terrestrial between mosses on rather exposed coastal sand-dune.

TYPE.—THE NETHERLANDS, prov. Noord-Holland, Island of Texel, the 'Slufter', 29 Oct. 1976, *Dr. F. Tjallingii & Mrs. G. Tjallingii-Beukers*.

Because of the structure of the pileipellis, viz. no true Rameales-structure, and the size of the spores this species has to be placed in section *Dealbati* Sing. 1973. Considering only the temperate species, its closest relative is *M. vaillantii* (Pers. ex Fr.) Sing. (syn.: *Marasmius languidus* Lasch sensu Kühn. & Romagn. 1953), a quite common species in the Netherlands growing on branchlets and fallen leaves. The latter differs from the species here described particularly in the size and shape of the spores and the cheilocystidia. The covering of the stipe of *M. pachycraspedum* resembles very much that of *M. tricolor* (Alb. & Schw. ex Fr.) Sing. In that species however the pileipellis has a well-developed Rameales-structure.

I wish to thank Dr. R. A. Maas Geesteranus for preparing the Latin diagnosis, and Dr. C. Bas for critically reading the manuscript of this paper.

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NEWLY RECORDED IN THE NETHERLANDS—III*
TYROMYCES SEMISUPINUS

H. F. VAN DER LAAN
Arnhem, The Netherlands

TYROMYCES SEMISUPINUS (Berk. & Curt.) Murr.

Polyporus semisupinus Berk. & Curt. apud Berk. *in* Grevillea **1**: 50. 1872. — *Tyromyces semisupinus* (Berk. & Curt.) Murr. *in* N. Am. Flora **9**: 34. 1907. — For other synonyms see Donk (1974: 180).

Fruitbodies resupinate to effused-reflexed or in the shape of sessile, dimidiate pilei, measuring up to 4 × 2 × 0.2–0.3 cm, often narrowed at base, with acute edge. Upper surface rough, whitish, locally brownish. Resupinate parts with white tomentose margin or fertile up to well defined edge. Context and very thin subiculum white, tough, coriaceous when fresh, rigid after drying. Tubes 1–2 mm long; pores angular, 0.15–0.25 mm in diam., 4–6 per mm; dissepiments very thin; pore surface cream to light yellow when fresh, (light) orange after drying.

Hyphal system dimitic. Generative hyphae thin- to thick-walled, 1.5–4 µm in diam., rarely to frequently septate, with clamps, rarely to frequently branched. Skeletal hyphae thick-walled, abundant, in context interwoven, 4–5 µm in diam., in dissepiments largely parallel, 3–4 µm in diam. Basidia club-shaped, 2–4-spored, (8–)9–15 × 3–4.5(–5) µm. Spores ellipsoid, flattened at one side, hyaline, smooth-walled, inamyloid, 3–4(–5) × 1.5–2.5 µm.

COLLECTIONS EXAMINED.—THE NETHERLANDS: prov. Drente, Westerbork, Mantingerbos, 7 Sept. 1972, *J. J. Barkman*, on dead, fallen stem of Betula (WBS); prov. Gelderland, Otterlo, Nat. Park 'De Hoge Veluwe', 15 Nov. 1975, *J. Geesink*, on Pinus (herb. Geesink); Arnhem, Warnsborn, 28 Aug. 1976, *H. F. van der Laan*, on dead, fallen branch of deciduous tree (L).

Recording the occurrence of the species in the Netherlands is the only purpose of this note. For that reason, I have not gone into its systematic position, which seems to be uncertain, and adhere to the name most frequently used in literature.

Tyromyces semisupinus is widely distributed in the northern part of the temperate zone of the northern hemisphere, but is generally considered a rare species. Jahn (1970/71: 62), however, states that it is common in eastern Westphalia. He is of the opinion that it has been overlooked often in other parts of West Germany, where it has been recorded but a few times. Pegler (1973: 33) lists *T. semisupinus* for Great Britain. Jahn (ibid.) reports its occurrence on [trees on] all kinds of soils (auf allen

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* Nr. I, entitled '*Poria lindbladii* found in the Netherlands', was published in Persoonia **8**: 331–332 (1975) and Nr. II, entitled '*Schizopora phellinoides* in the Netherlands' in Persoonia **9**: 155–156 (1976).

Böden), but the three known collections from the Netherlands all are from poor, acid, sandy soils.

The author wants to express his gratitude to Dr. J. J. Barkman and to Mr. J. Geesink for kindly permitting study of their collections and publication of the results.

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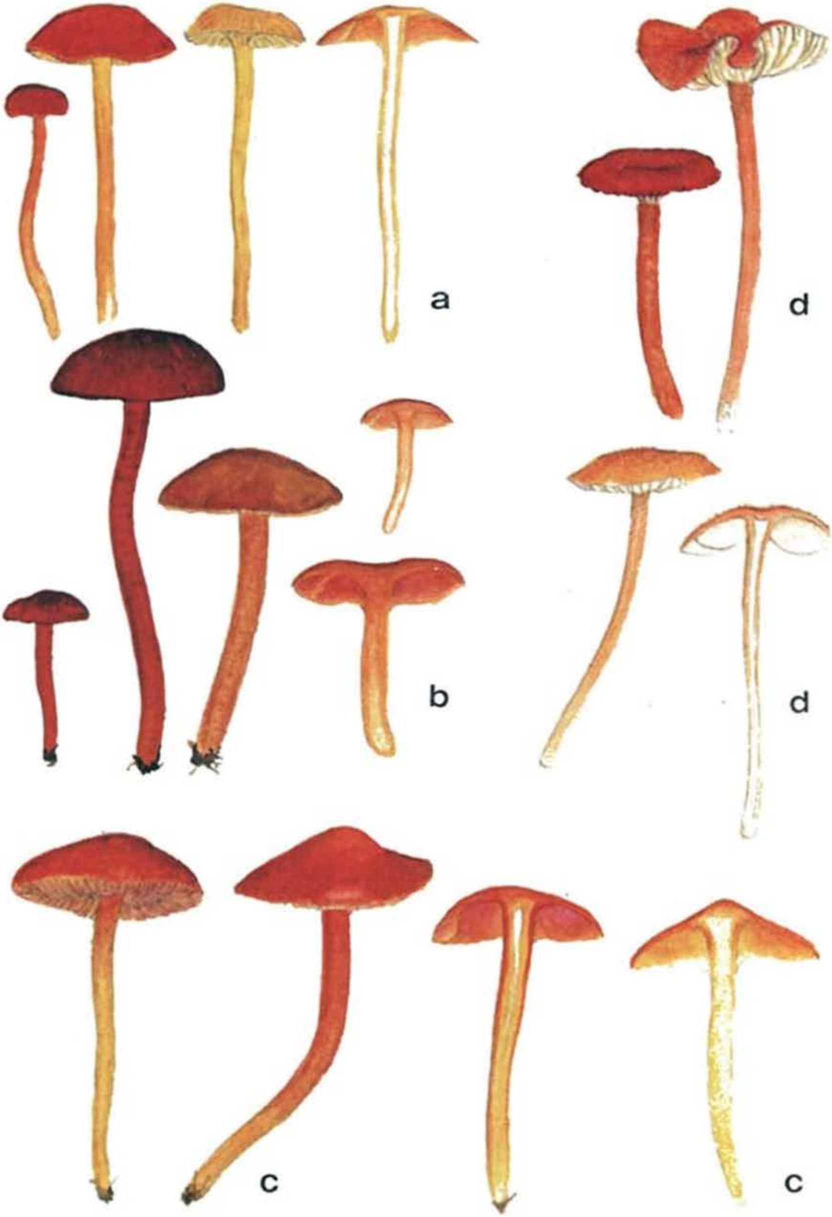
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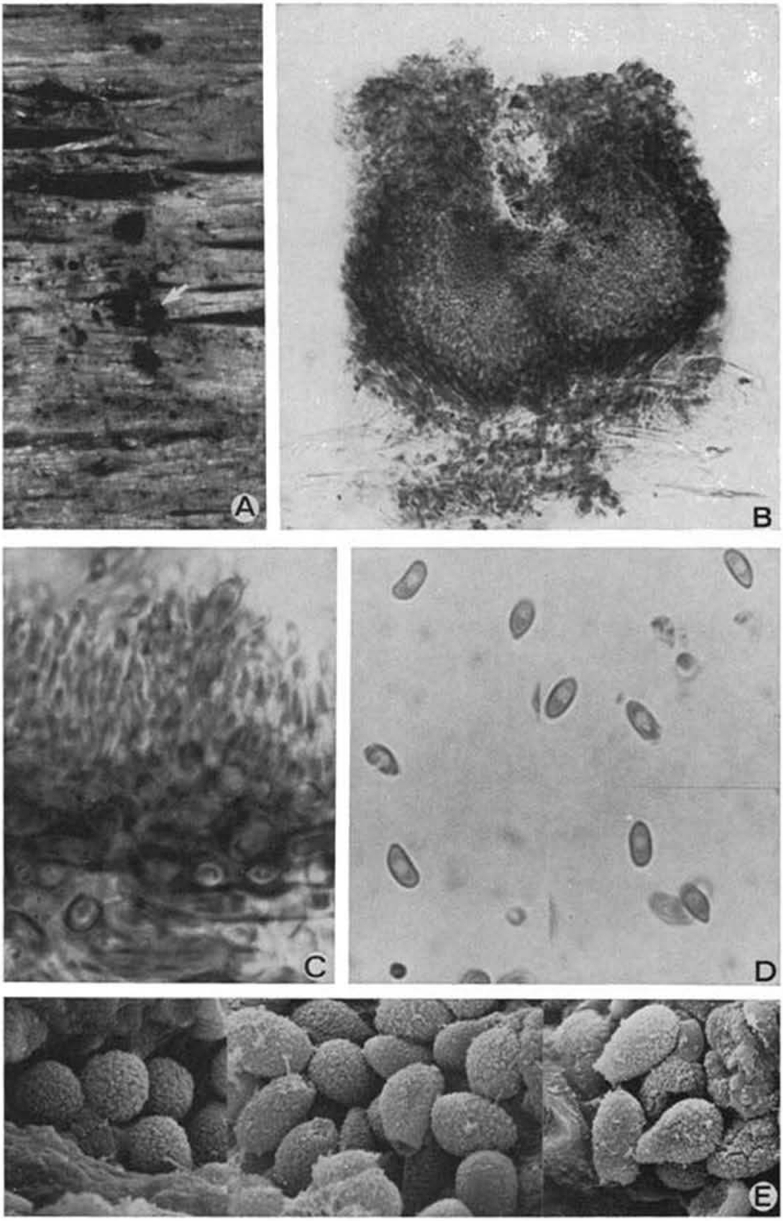

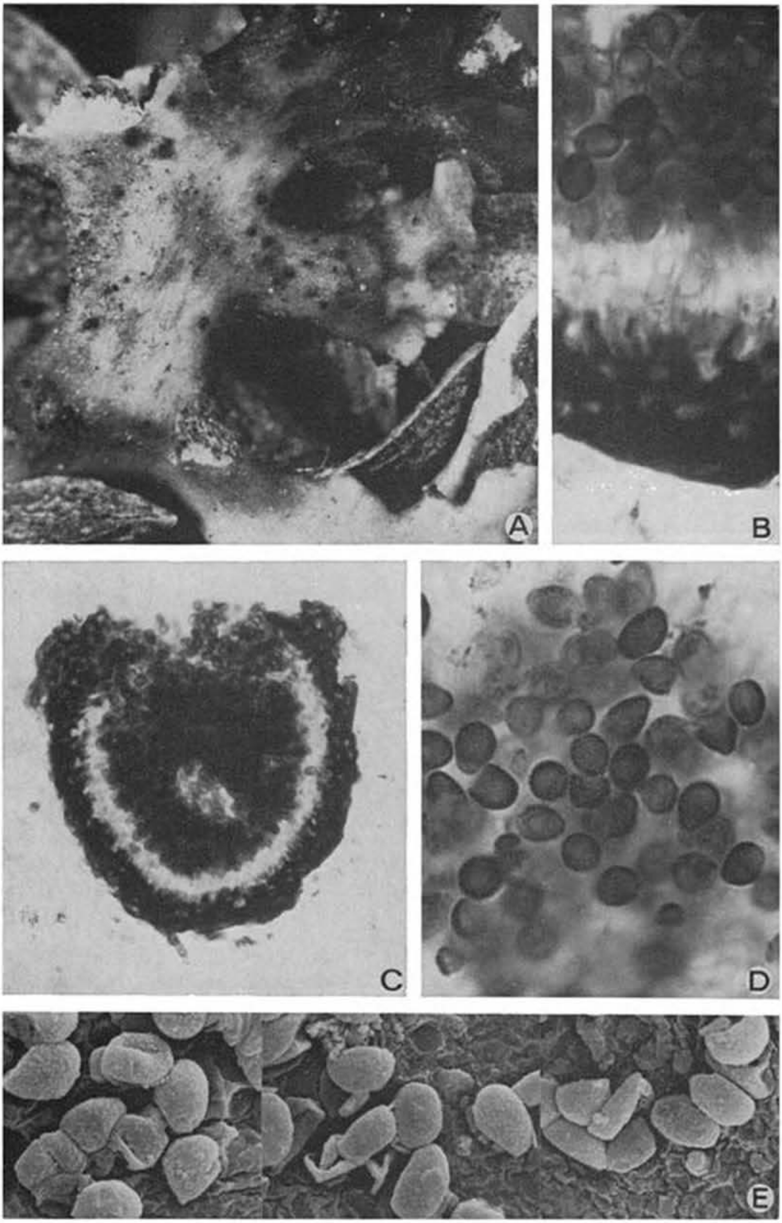
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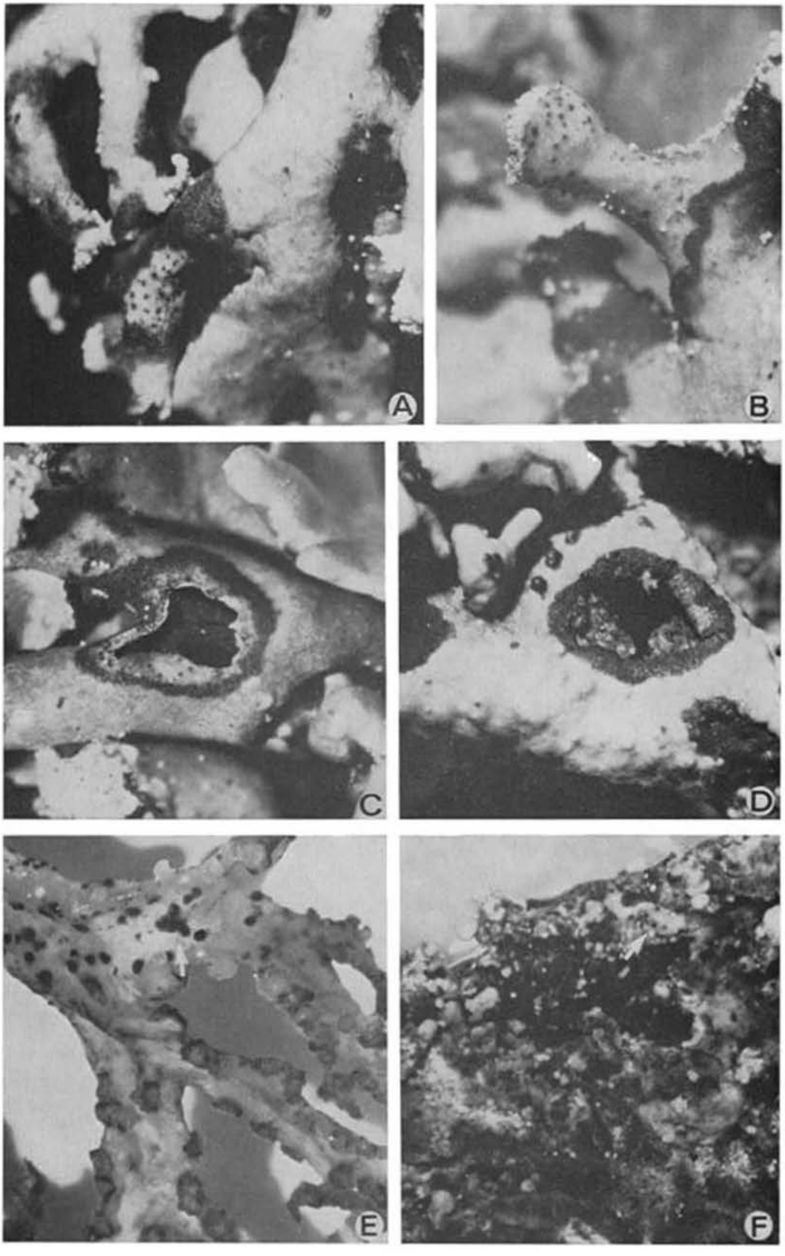

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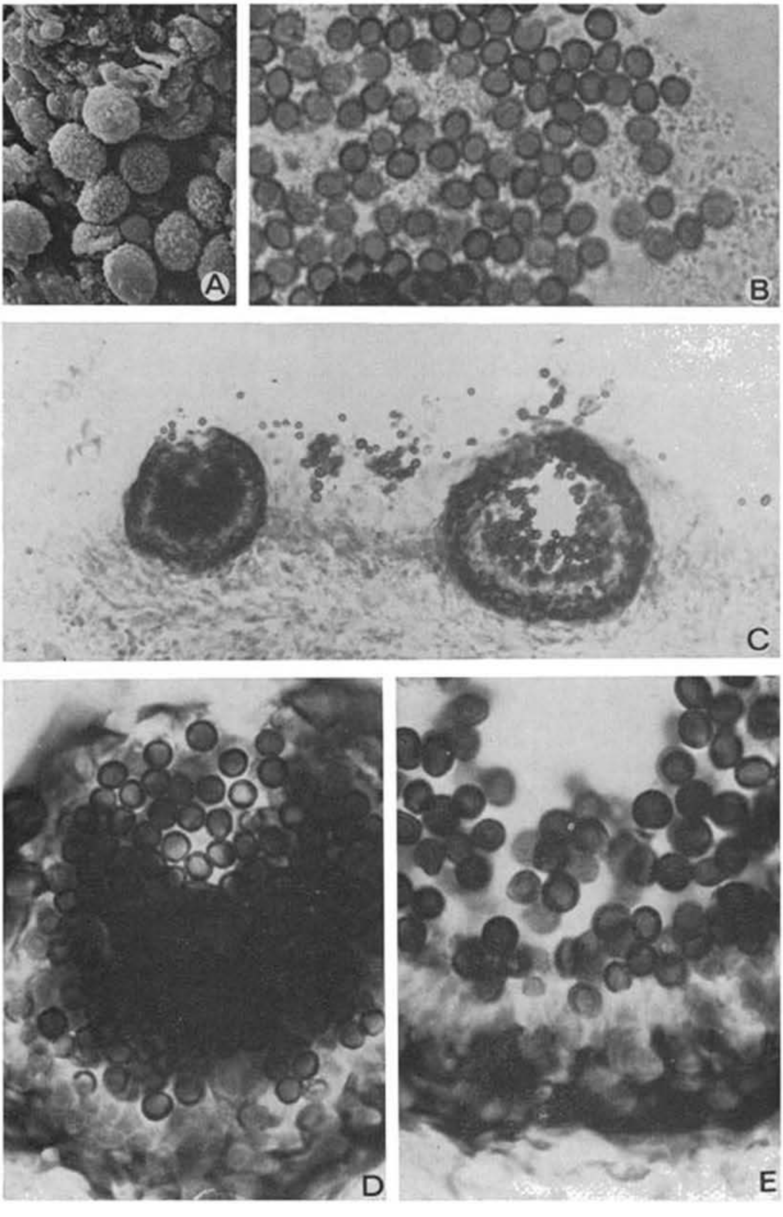

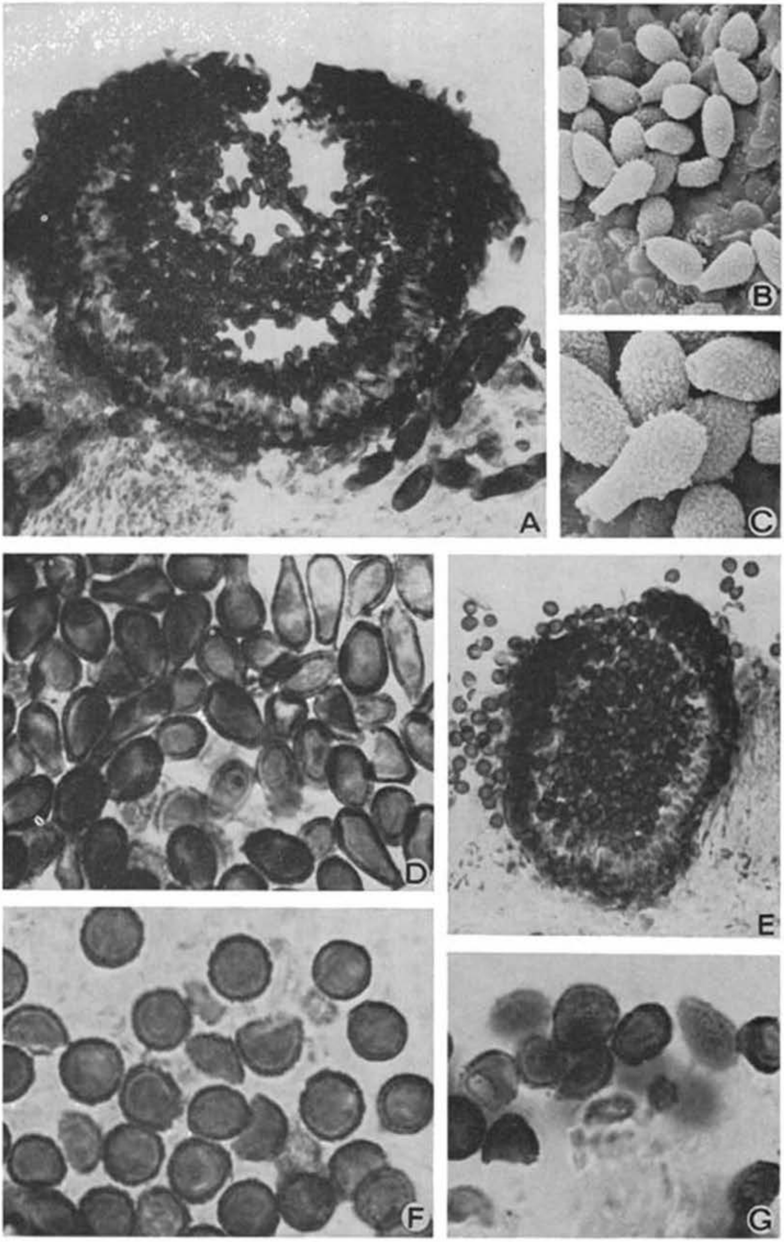
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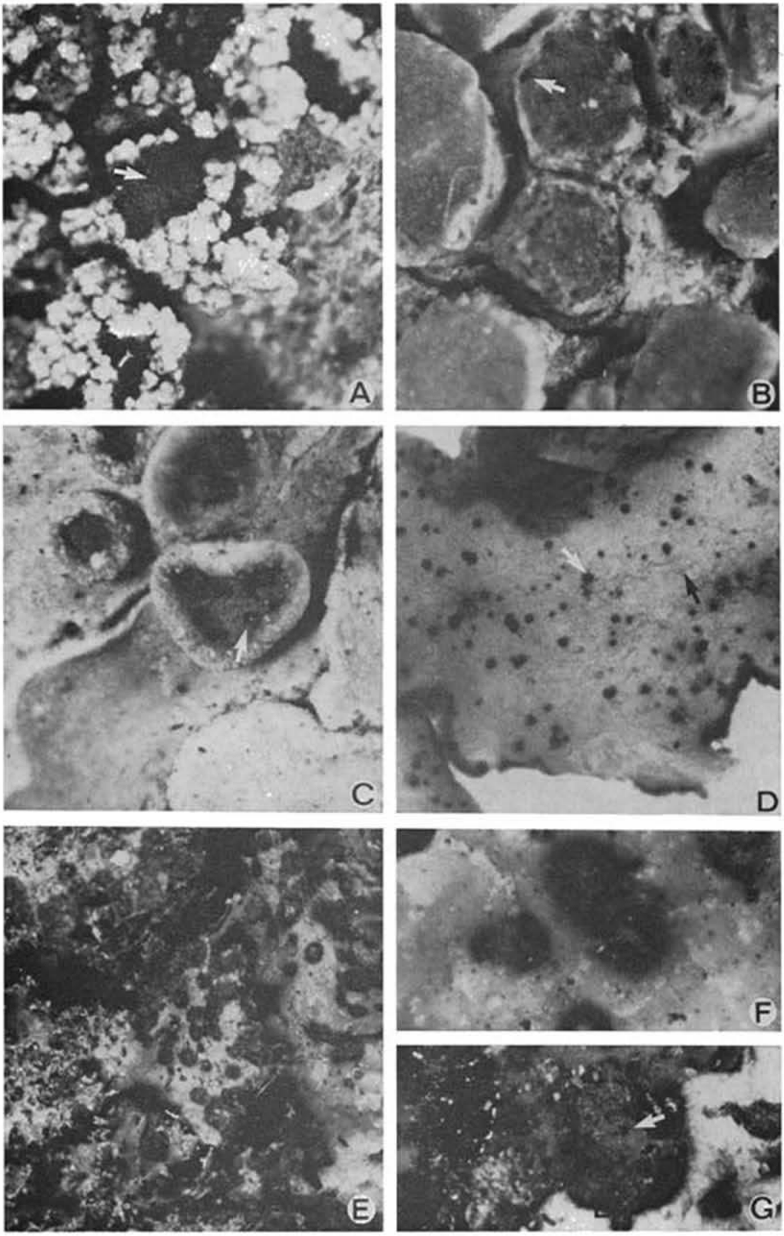
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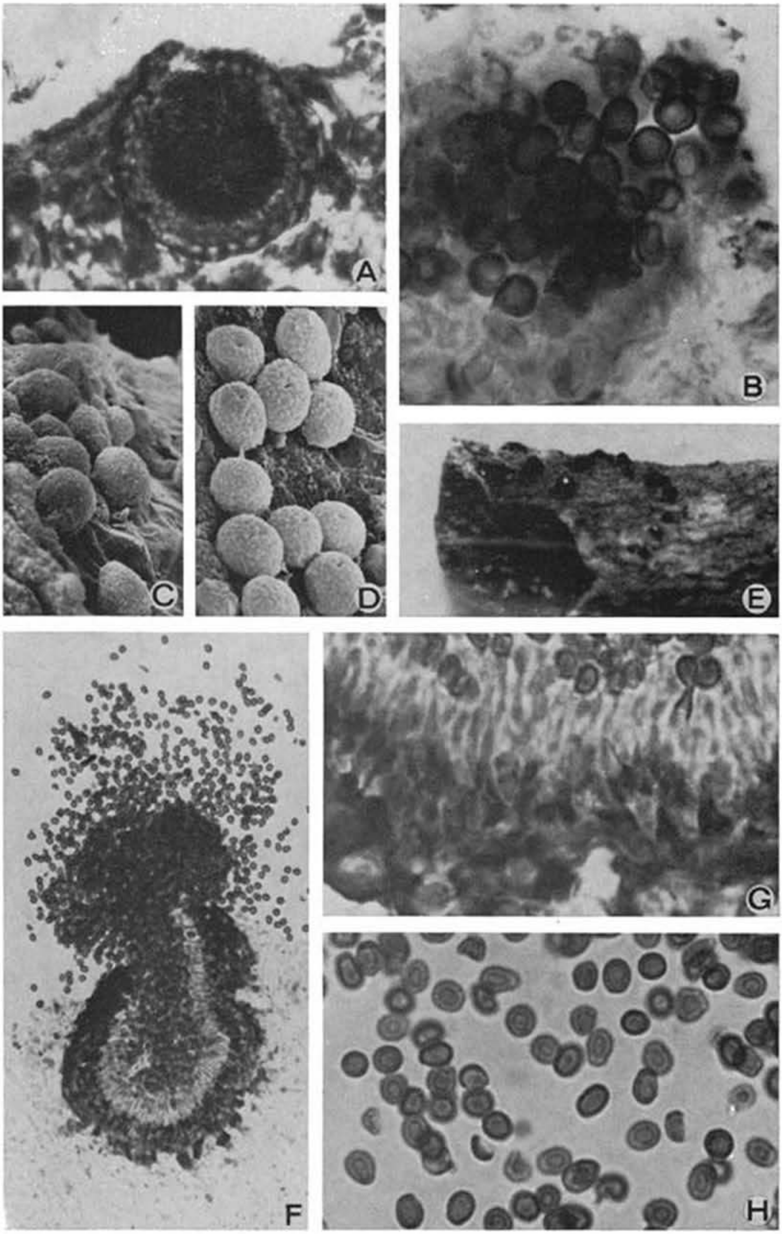
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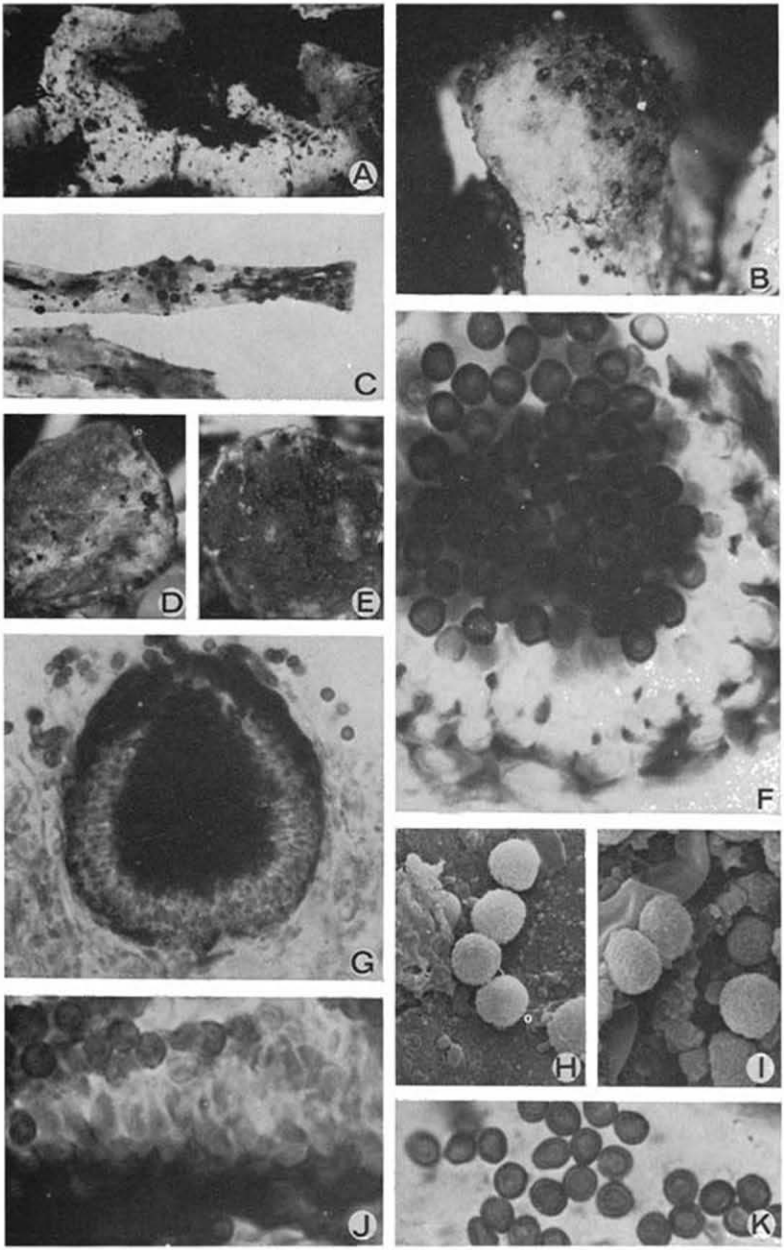
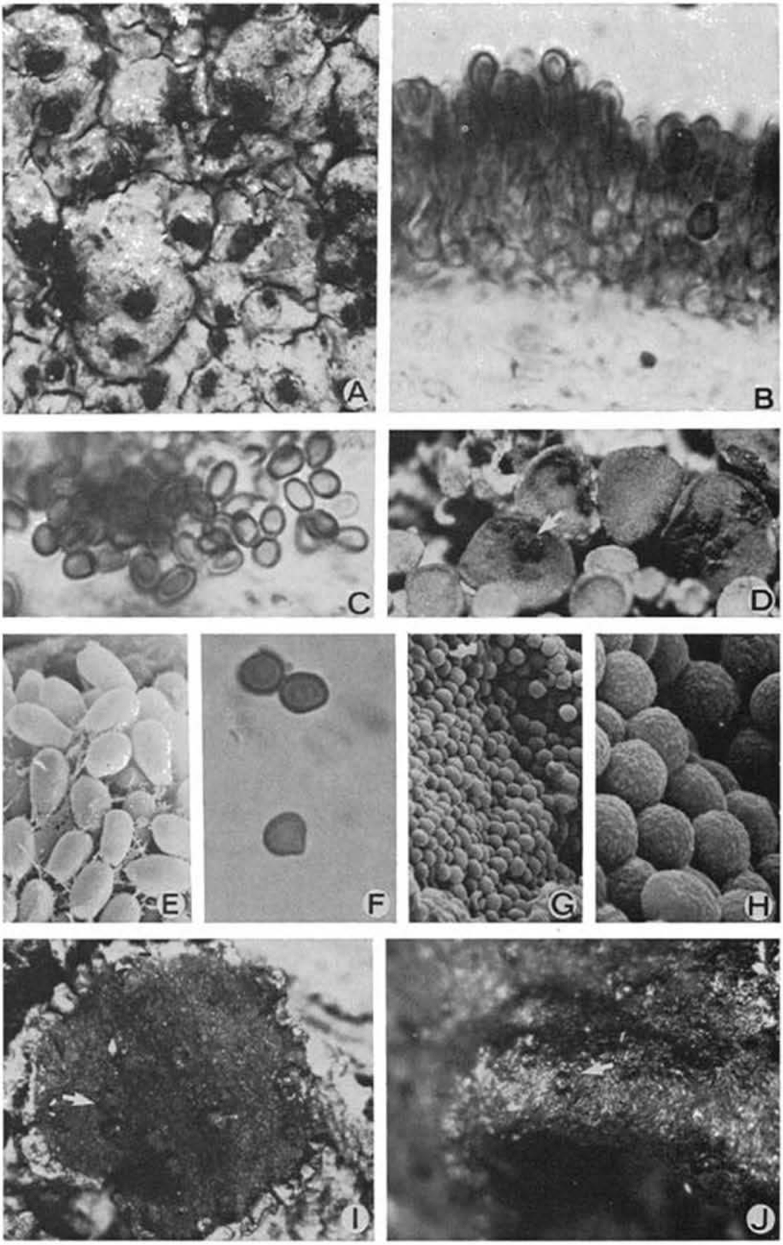
G
H


A
B
C
D
E
F
G
H
I
J
K


A
B
C
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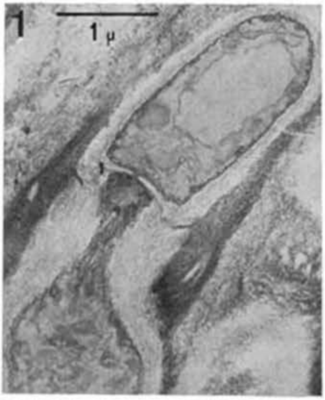
J

1



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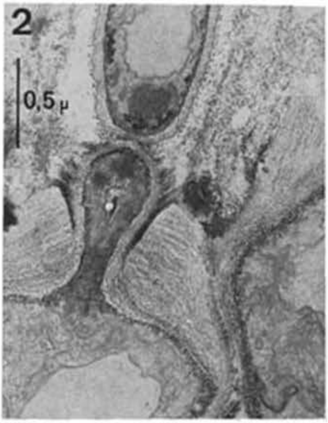

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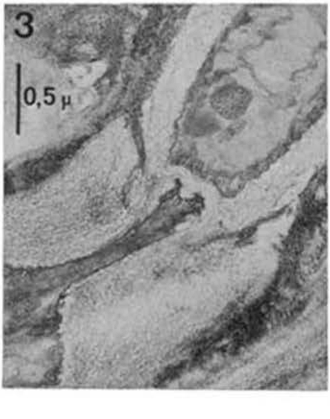
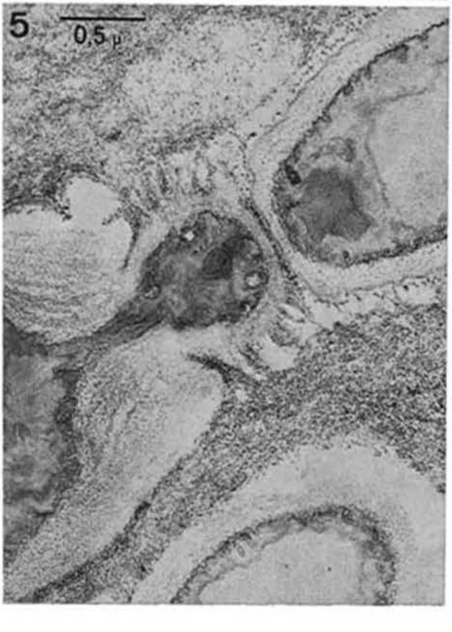


4

5

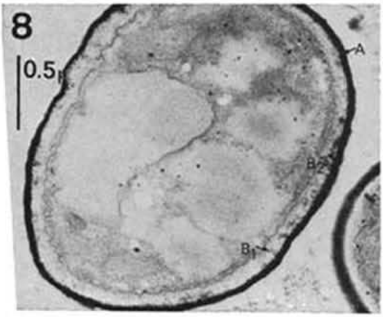


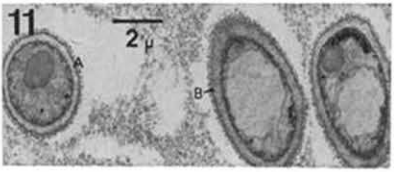

6
1 μ


9
1 μ


7
1 μ


10
1 μ


8
0.5 μ
A
B2
B1


11
2 μ
A
B