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TAXONOMIC AND BIOLOGICAL OBSERVATIONS ON THE GENUS LICHENOCONIUM (SPHAEROPSIDALES)

D. L. HAWKSWORTH*
Commonwealth Mycological Institute, Kew

(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

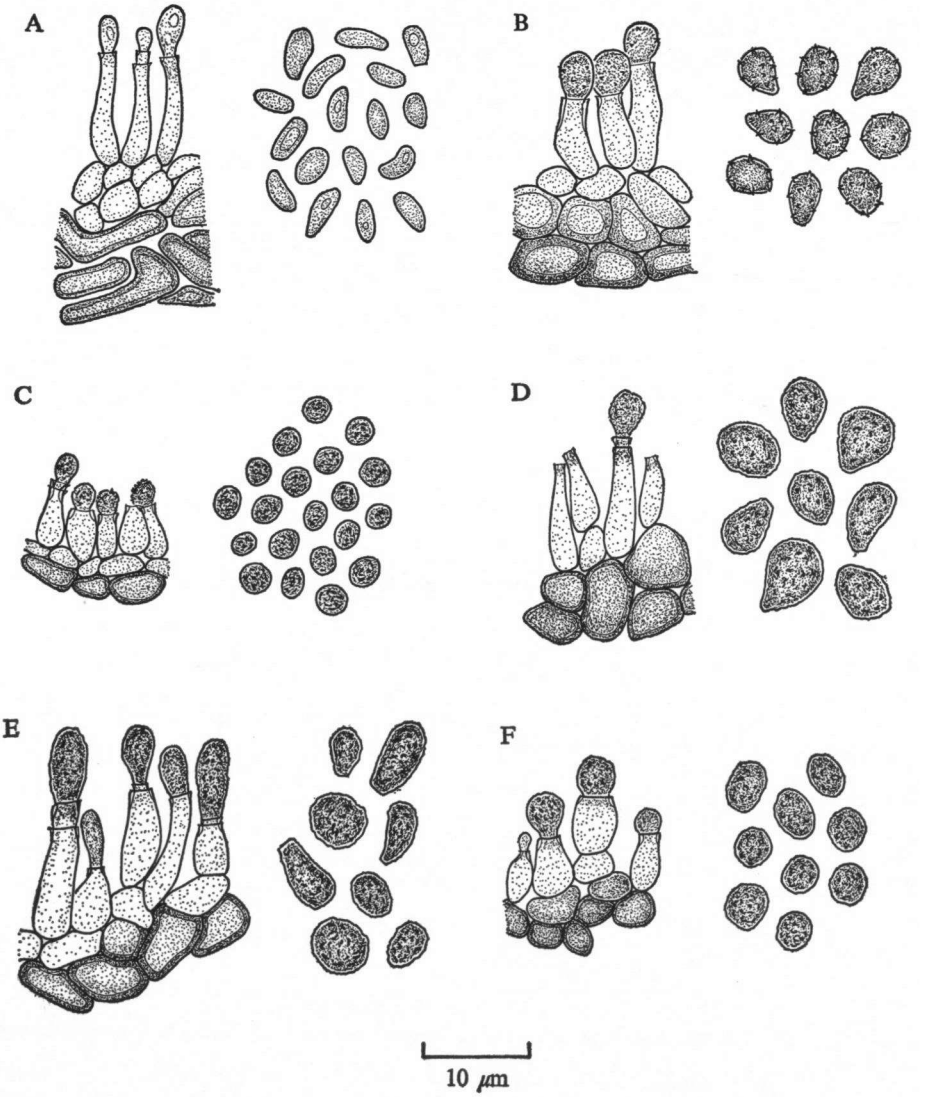

Fig. 1. Conidiogenous cells and conidia of *Lichenoconium* species. — A. *L. boreale* (holotype). — B. *L. echinosporum* (holotype). — C. *L. erodens* (holotype). — D. *L. cargillianum* (holotype). — E. *L. lichenicola* (holotype). — F. *L. parasiticum* (*IMI 192264*).

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

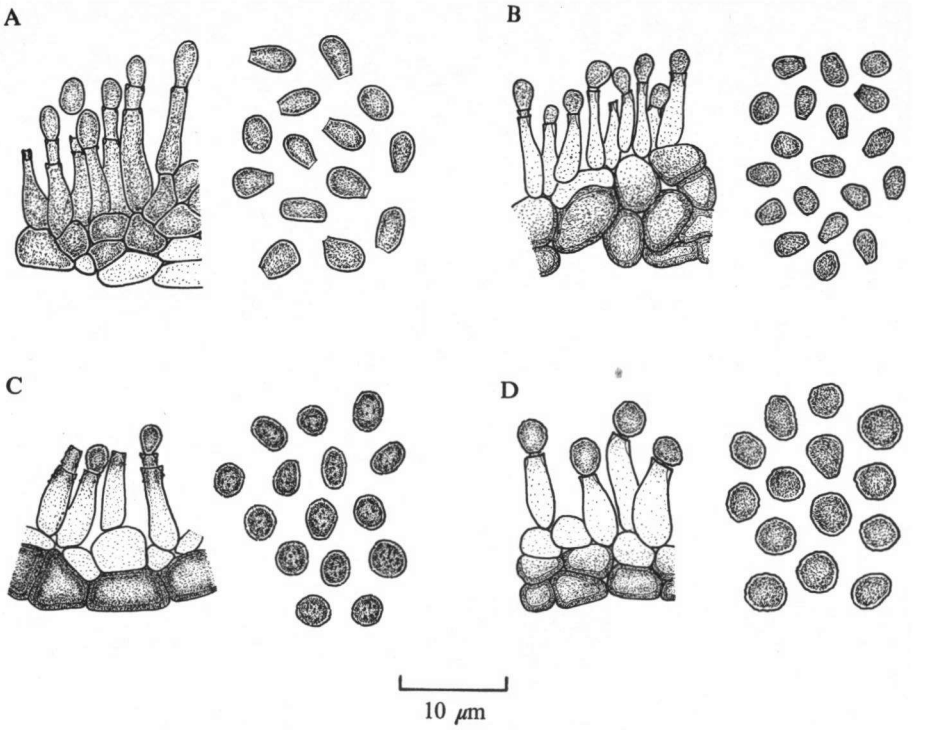

Fig. 2. Conidiogenous cells and conidia of *Lichenoconium* species. — A. *L. pertusariicola* (*IMI 186240*). — B. *L. pyxidatae* (holotype). — C. *L. usneae* (isotype). — D. *L. xanthoriae* (holotype).

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.

* 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 annellidelike 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 *Lecanorae 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 rocks at the lake Ånnsjön, alt. 525 m, 22 Feb. 1957, *R. Santesson 11684* (UPS).

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 Vouauxls 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 21&c* (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 blacke-

ned 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 be-

coming 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

c l a d o n i a e. — *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.

r e s i n a e. — *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.

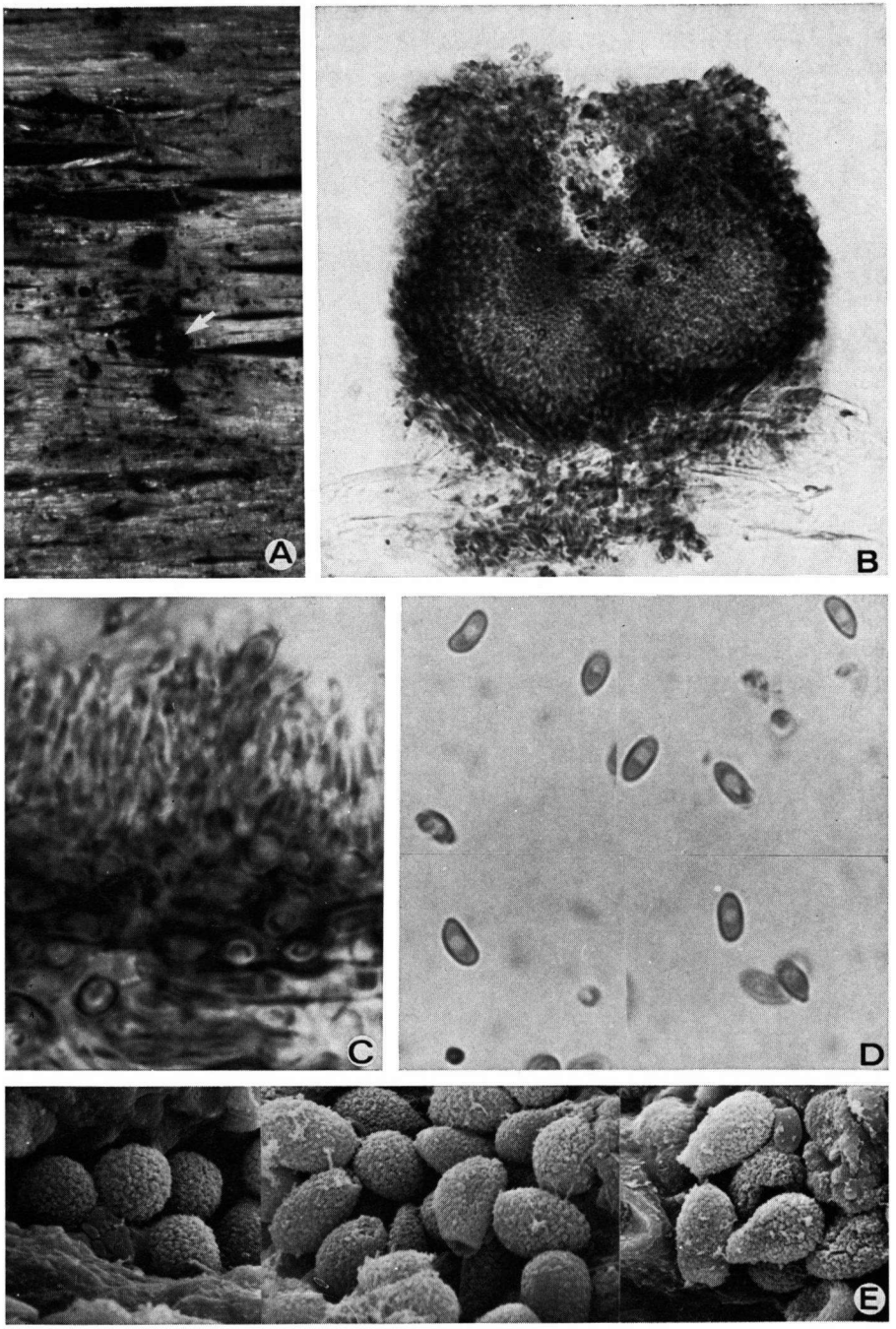
PLATE 29

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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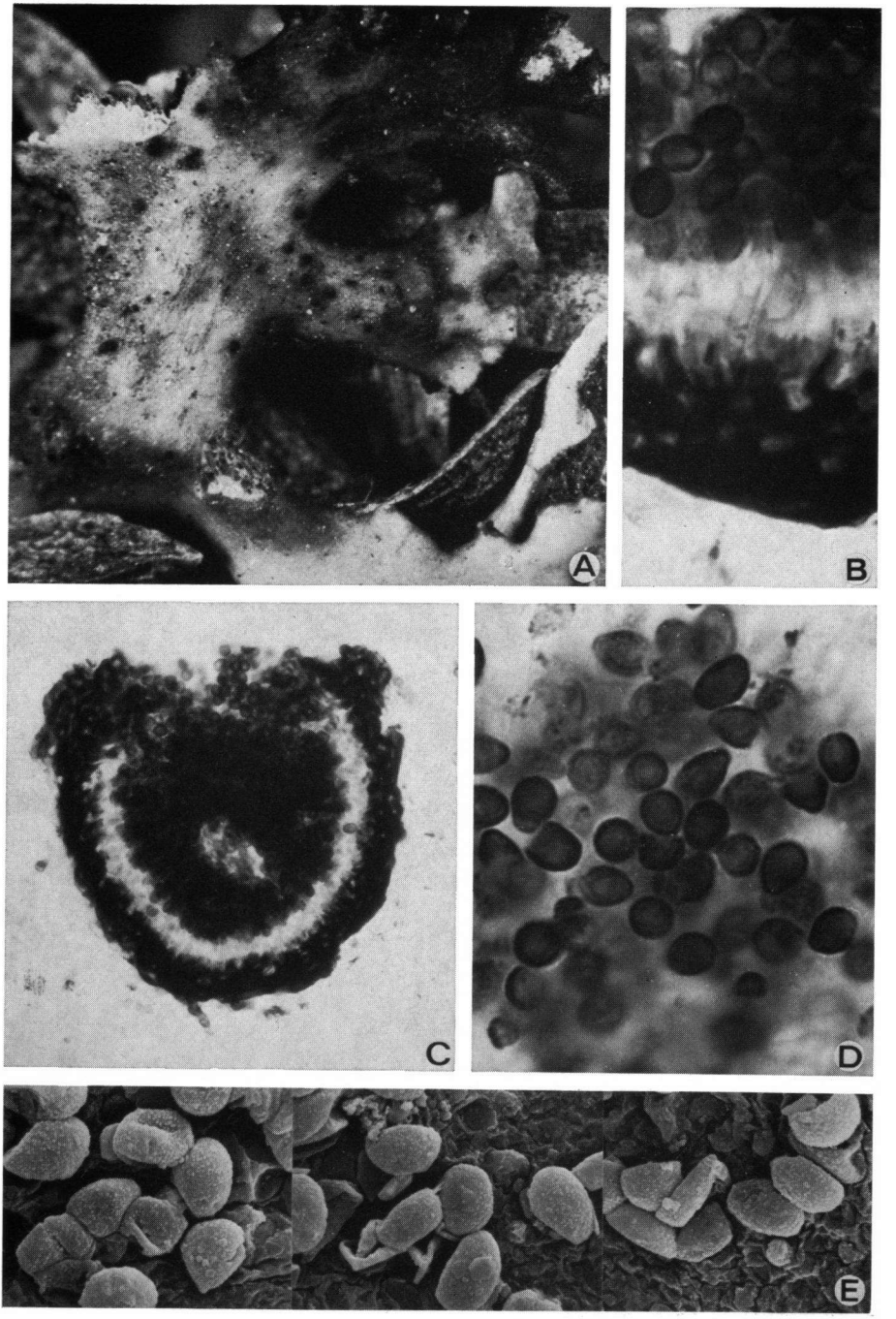
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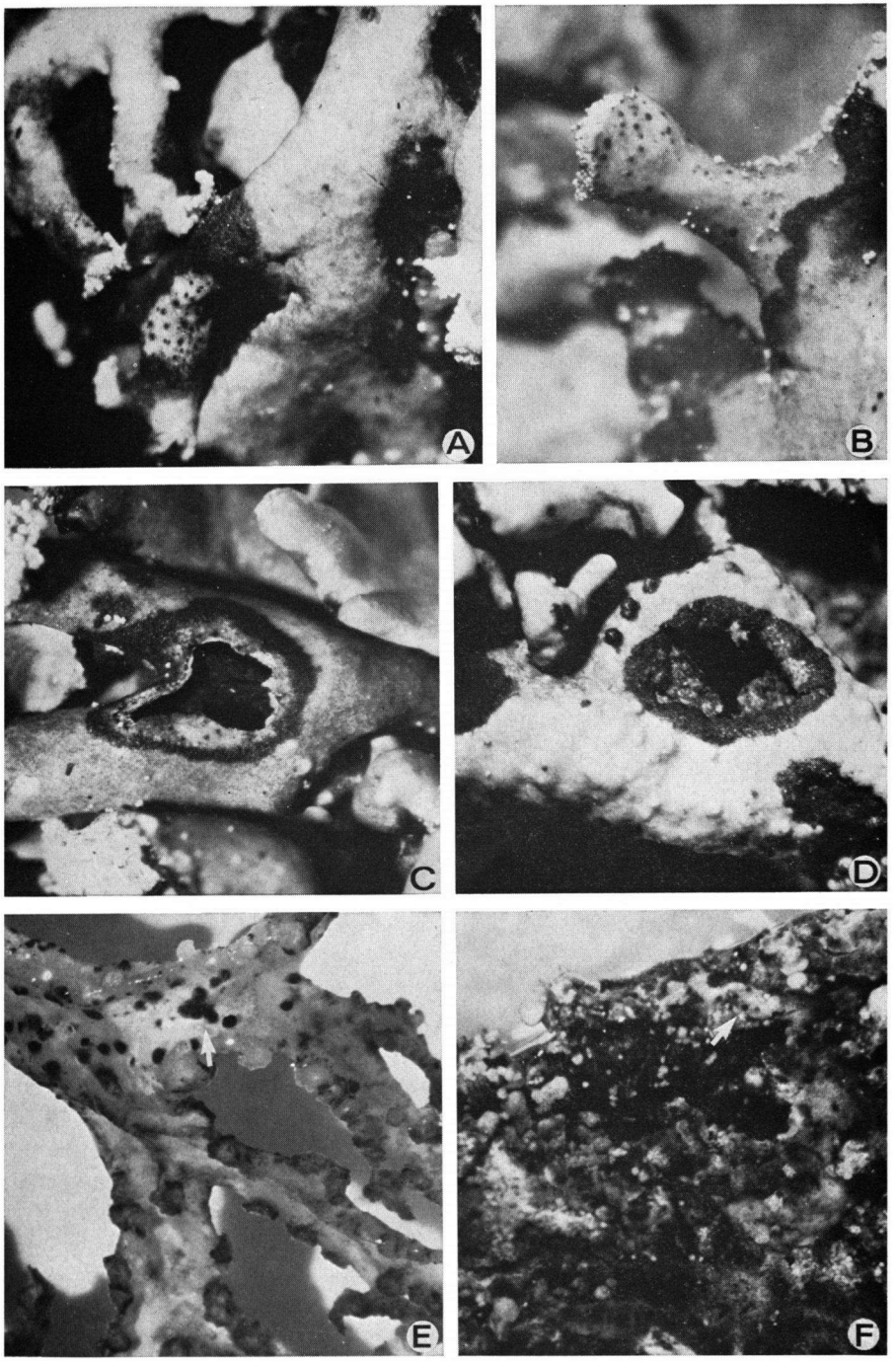
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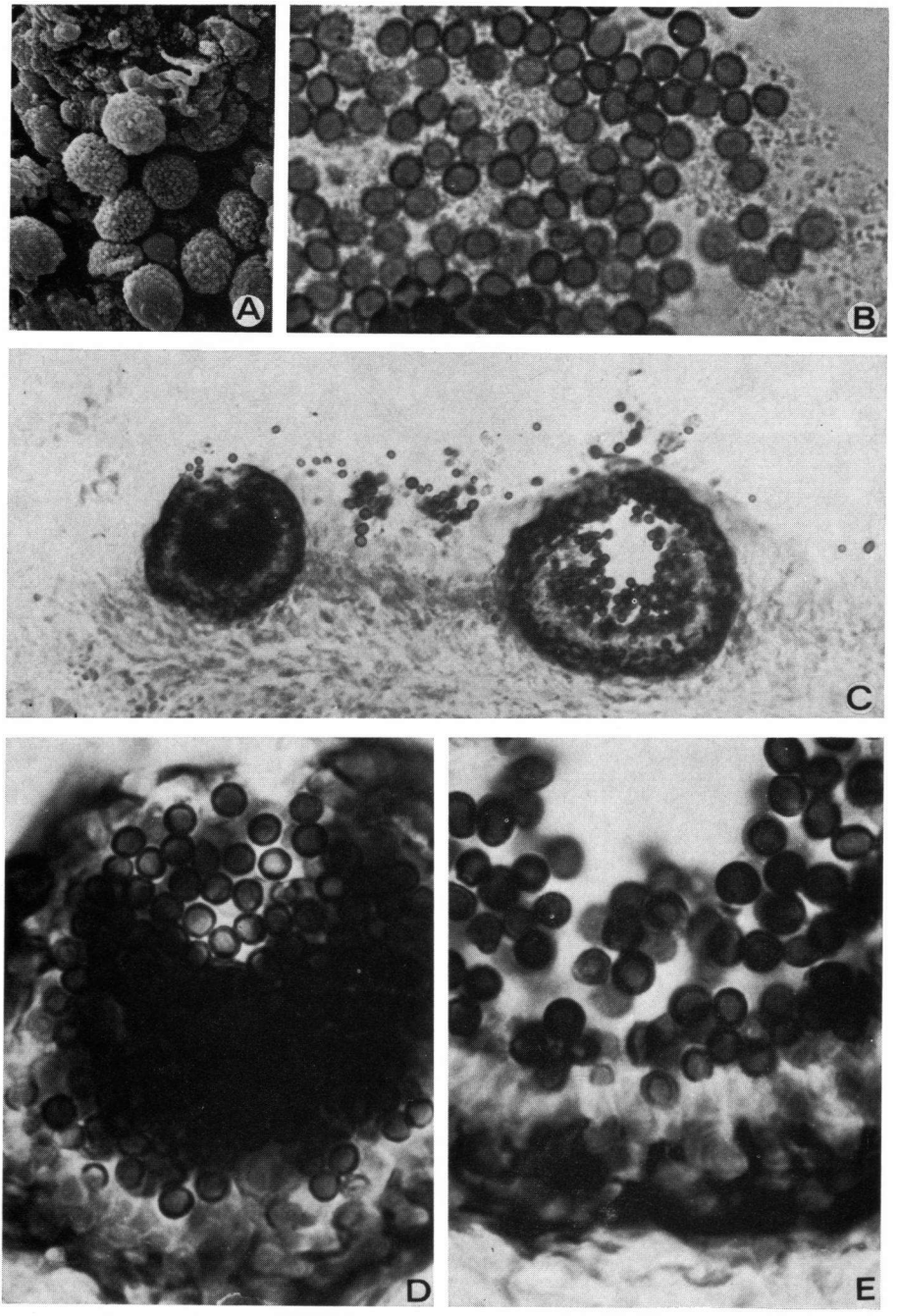
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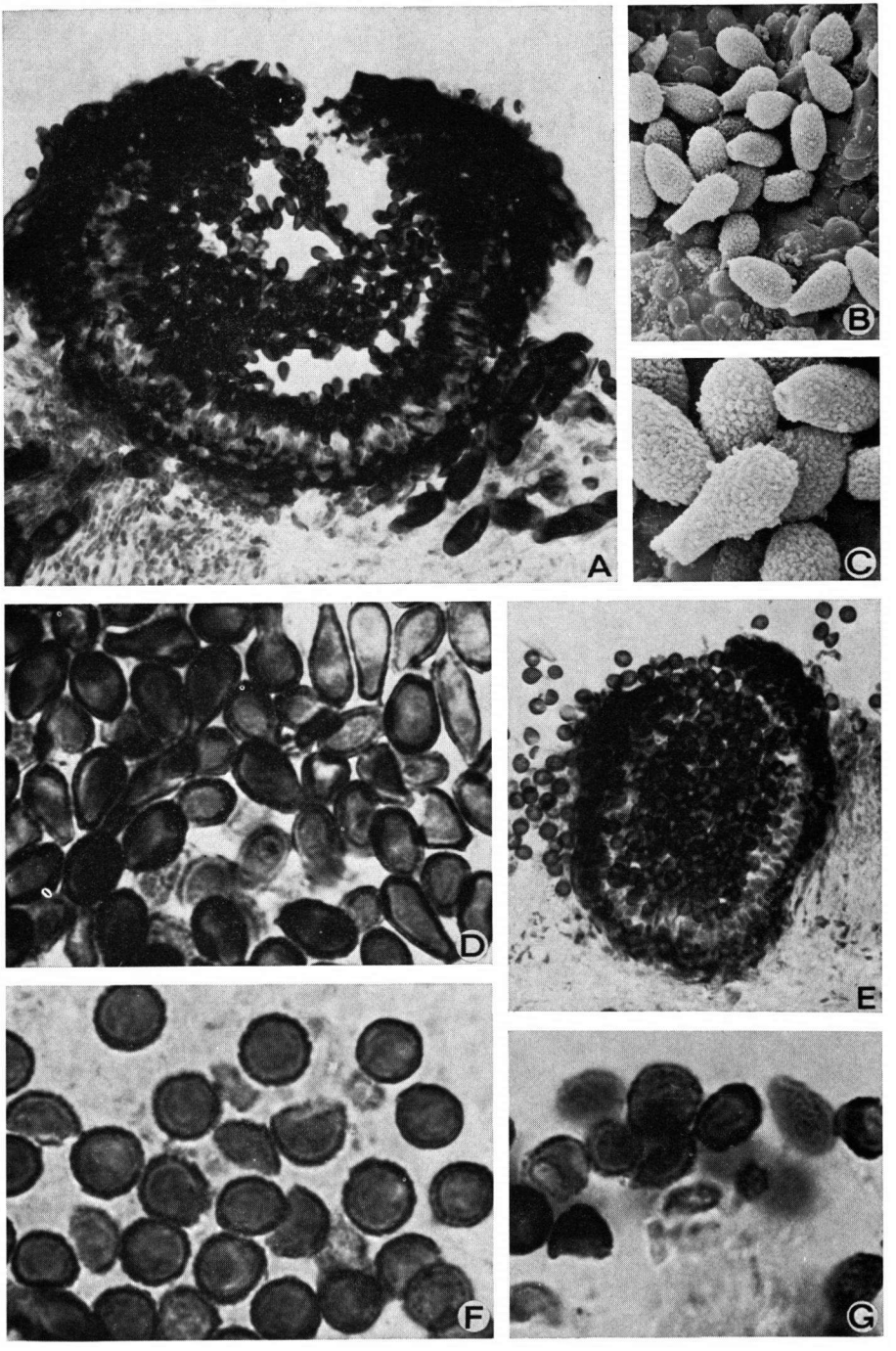
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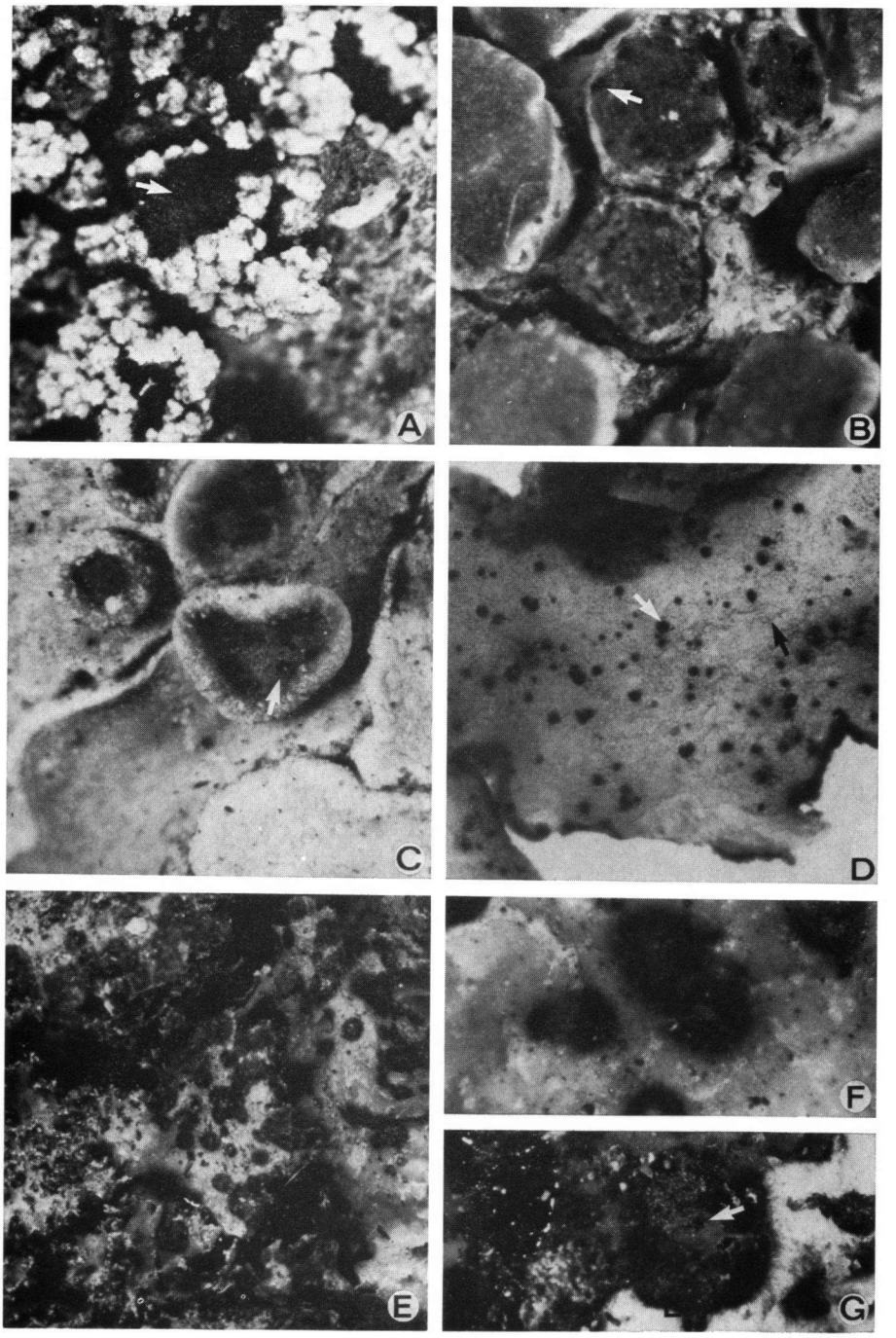
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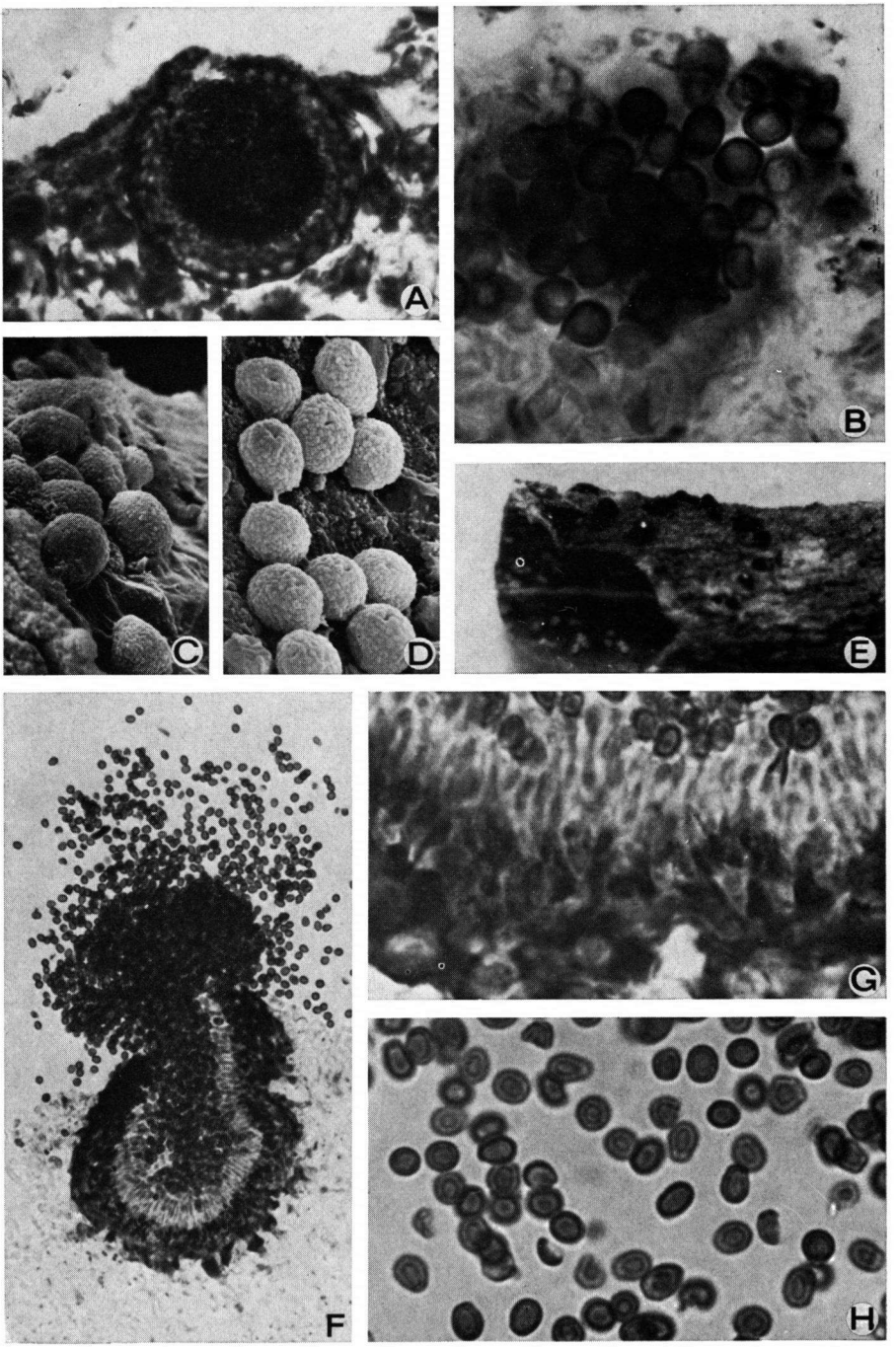
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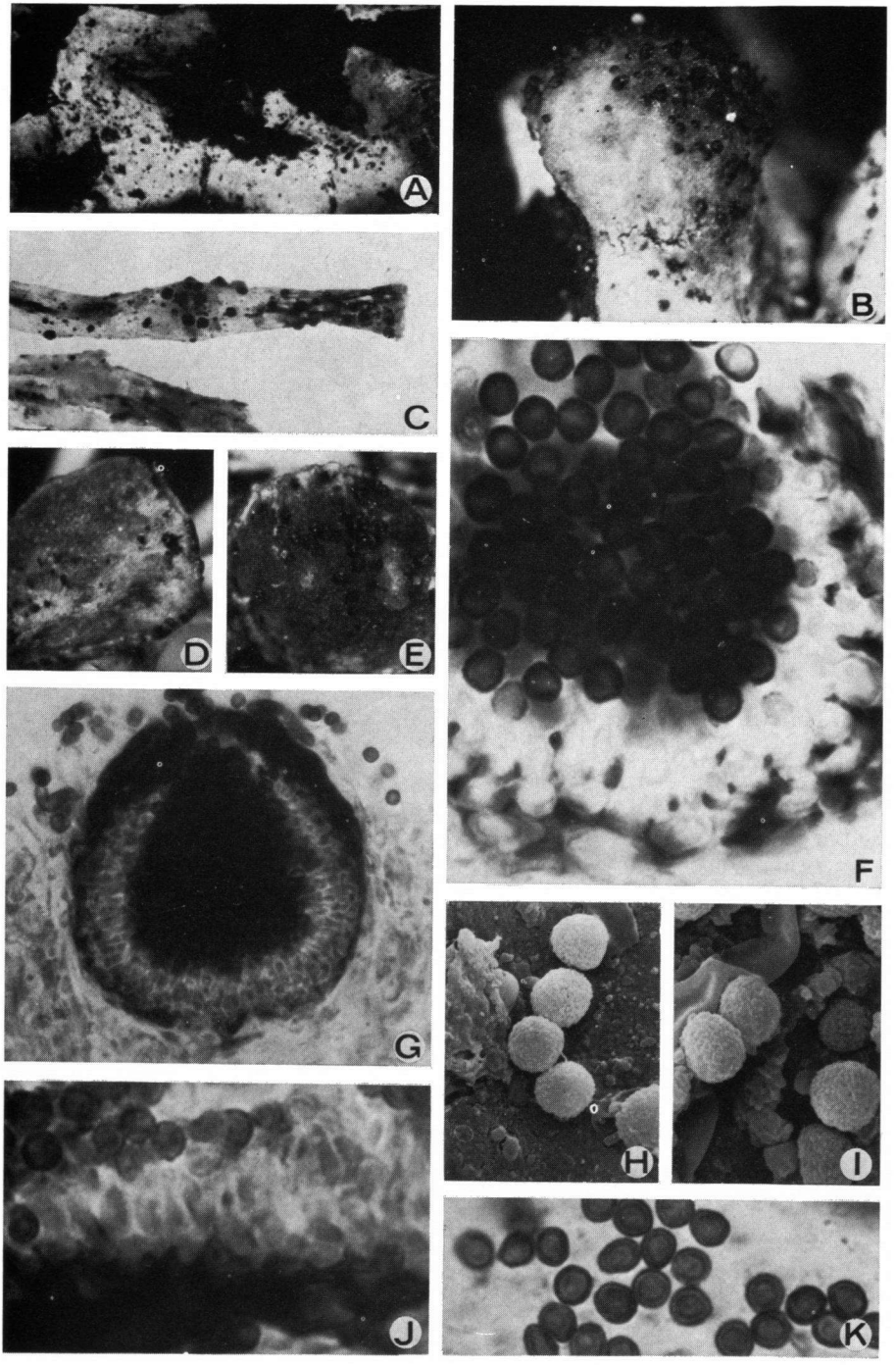
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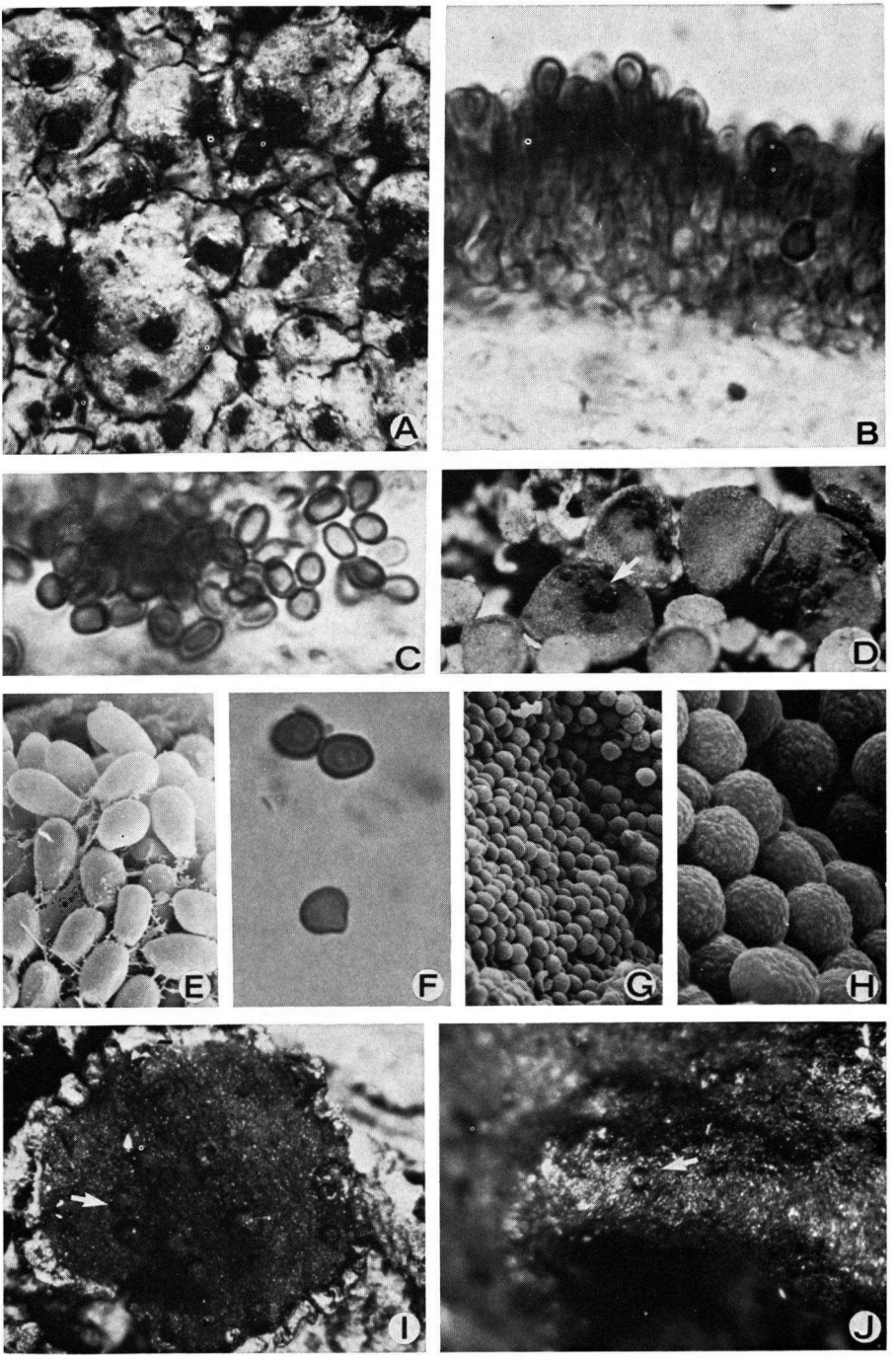
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