

## STUDIES OF PYRENOAMYCETES

## IV. NECTRIA (part 1)

By C. BOOTH

*Commonwealth Mycological Institute*

**T**HIS paper deals with the life histories of the British *Nectria* species. In a further paper now in preparation the predominantly tropical *Nectria* species will be described.

The name *Nectria* was first proposed by Fries (1825). Under 'Order 1 *Sphaeriacei*; Sub-order *Sphaerini*; genus *Hypocrea*' he erected the following four sections: A. *Cordyceps*; B. *Hypocrea*; C. *Hypomyce*; D. *Nectria*; the latter with 'Perithecia superficialia subiculo tomentoso imposita aut omnino libera'. It should be noted that this diagnosis must include certain *Hypomyces* species together with the discrete astromatic *Nectria* spp.

De Notaris (1844) accepted the Fries classification but changed the name to *Hypocreacei*; he suggested that the four sections proposed by Fries should be regarded as distinct genera. However, it remained for Fries (1849) to erect *Nectria* as a distinct genus when he gave the following diagnosis: 'Peritheciis liberis, membranaceis (neque corticatis nec pruina velatis) flaccidis, laete coloratis, papilla pallida, nucleo fluxiti pallido guttae 1, floccorum alborum instar expulsae, asci 8-sporis sporisque pellucidis.'

Thus, as Fries conceived the genus, it is based on structure, colour, and texture of the perithecium. In a footnote he states that it includes species whose asci are variable and whose ascospores range from simple to filiform.

We owe our modern conception of the genus to Saccardo (1878) who restricted *Nectria* to species with 1-septate hyaline ascospores and gave the following diagnosis: 'Perithecia erumpenti-superficialia v. superficialia, caespitosa v. discreta, saepe stromate pulvinato, primitus conidiophoro insidentia, rosea v. laete colorata. Asci cylindranei v. fusoidei, initio infra apicem coarctati. Sporidia ellipsoidea v. oblonga, 1-sepatata, hyalina, loculis typice non secedentibus.'

Saccardo segregated the diverse species which had been placed in the genus *Nectria* on the artificial but usually workable basis of spore septation, shape, and colour. The exception to this is the genus *Sphaerostilbe*, where he followed Tulasne and Fuckel in basing the genus on the presence of the conidial fructification. Within his separation on spore characters, Saccardo also recognized the Friesian distinctions of position of perithecia with reference to the stroma and substratum. This, of course, led to the erection of the many new genera in the Hypocreaceae described by Saccardo.

In spite of this segregation, when Saccardo (1883) compiled *Nectria* in the *Sylloge Fungorum* he accepted 145 species, which he arranged in the following subgenera:

1. *Eu-Nectria*: perithecia caespitose on a stroma; glabrescent.
2. *Dialonectria*: perithecia subdiscrete; glabrescent.
3. *Hyponectria*: perithecia glabrous but on a byssoid subicle.

4. *Lepidonectria*: perithecia scaly.
5. *Lasionectria*: perithecia minutely pilose.
6. *Cryphonectria*: perithecia subimmersed in a crustose stroma.
7. *Cosmospora*: ascospores verrucose, rufescent.
8. Species minus cognitae.

Since 1883, mycologists have accepted Saccardo's classification with minor alterations and additions. Cooke (1884) raised *Dialonectria* to generic rank in his *Synopsis Pyrenomycetum* and this genus has been frequently used in Britain. The rest of Cooke's classification has been largely ignored.

Seaver (1909) reverted to a refinement of the Fries method. He recognized the two families Hypocreaceae and Nectriaceae. The latter he divided into two tribes:

1. Nectriaceae—superficial or erumpent non-stromatic perithecia.
2. Creonectriaceae—superficial caespitose perithecia formed on a more or less conspicuous conidial stroma.

Seaver's *Nectria* corresponds to Cooke's *Dialonectria* and *Creonectria* to the genus *Nectria*.

The fundamental objection to Seaver's classification was pointed out by Theissen and Weese, who emphasized that the presence or absence of a stroma is a character which varies in some species with the nature of the substratum on which it develops. In *Nectria coccinea* the stroma is absent when the perithecia develop on hard wood but well developed when they occur on bark. Most of the available evidence supports the view that the archicarp arises in a stroma, which in the mature perithecium may be represented only by the outer region of the perithecial wall, or may be well developed.

Theissen (1911), identifying *Nectria* species from Brazil, went further than Saccardo in using spore characters as a basis of separation within the genus, for he proposed three sections based on the appearance of the outer ascospore wall:

- A. *Leiosporae*—spores smooth, not lineated or warted.
- B. *Rhabdotosporae*—spore membrane longitudinally striate.
- C. *Cosmosporae*—spore membrane warted.

Saccardo's classification is based on the compilation of the descriptions of the *Nectria* species published at that time and cannot in any sense be regarded as critical. *Nectria* species cannot be readily distinguished on the Saccardoan principles of size and shape of the perithecia, asci, and ascospores.

A usable classification must bring together related species which have been sufficiently well described to make their identification and separation possible. The application of Theissen's separation as a primary division of the British *Nectrias* results in cutting across the natural groups, and brings together species which have only the ornamentation of the spore wall in common.

The modern approach to the classification of *Nectria* has progressed along two lines. The first was begun by Höhnelt and Weese, working in Austria. They began a revision of *Nectria* at the species level and this work resulted in a large number of species names being reduced to synonymy.

Weese made a marked contribution to the taxonomy of this group when he

stressed the structure of the perithecial wall as a basis of separation within the genus. He was the first to emphasize the characteristic pseudo-palisade structure of the *Mammoidea* group.

Unfortunately, Weese never published any comprehensive classification based on his work, and his publications remain fragmentary and scattered. The first attempts to base a classification on perithecial wall characters were indecisive, but Miss Dingley (1951) was more successful when she used the perithecial wall structure as a primary character in the separation of the New Zealand *Nectria* spp.

The second line of approach to a modern classification of *Nectria* has been from a study of their conidial states. These were first mentioned by Tulasne, whose remarkable work on the pleomorphic nature of fungi was published in 1861-5. Fuckel (1870) also frequently mentioned the conidial states in his descriptions of *Nectria* spp. Both these workers based their evidence for the conidial state on the association of conidia and perithecia.

The first serious attempt to obtain cultural evidence of the conidial states of *Nectria* species was made by Brefeld and Tavel (1891); they described the conidia, at least the microconidia, from ascospore isolations of more than twenty *Nectria* spp.

However, the greatest progress in this line of approach was made by Wollenweber (1911-43). He spent many years on the monographic investigations of *Fusarium* species and in the course of this work he elucidated the life-histories of a large number of *Nectria* spp. The emphasis of Wollenweber's work was on the conidial state and he paid comparatively little attention to the perithecia. In 1926 he proposed a natural classification based on the morphology of the fungus as a whole, but in which the primary divisions were based on the structure and form of the conidial state.

The conidial states of the British *Nectria* spp. have been placed in the following imperfect genera: *Acrostalagmus*, *Cephalosporium*, *Ciliciopodium*, *Cylindrocarpon*, *Fusarium*, *Gliocladium*, *Myrothecium*, *Sphaeropsis*, *Stilbella*, *Stilbum*, *Tubercularia*, *Verticillium*, *Zythia*, and *Zythiostroma*.

These genera are normally assigned to the following four families in the fungi imperfecti: *Moniliaceae*, *Nectrioidaceae*, *Stilbellaceae*, and *Tuberculariaceae*. When viewed from this aspect these genera appear very diverse, but, in fact, a very close inter-relationship exists and there is no clear line of demarcation between them.

In the first place, they all have phialospores. In the genera with hyaline aseptate conidia the genera are based on the way the phialides are borne. In the simplest case, where the conidiophores are single lateral phialides on the mycelium, they are placed in the genus *Cephalosporium*. Where the conidiophores branch before bearing the phialides, we have the genus *Gliocladium*, unless the phialides are in whorls at each node of the conidiophore, in which case the species is assigned to the genus *Verticillium*. Where the branched conidiophores are aggregated on the surface of a stroma a sporodochium is formed as in *Tubercularia*; if the sporodochium is stalked, and therefore referred to as a synemma, we have *Stilbum* or *Stilbella*. Even in the conidial state of *Nectria cinnabarina* (*Tubercularia vulgaris*) the first phialides form below the surface and the outer layers of the stroma are then ruptured. If these outer layers persist, then a pyrenidium is formed as found in the genus *Zythia* or *Zythiostroma*.

Other genera owe their status to the morphology of the conidium. In *Myrothecium* they are dark. In *Fusarium* and *Cylindrocarpon*, although still remaining hyaline, they are elongate cylindrical and form transverse septa.

The use of conidial names should not be allowed to obscure the close relationship that exists between these species, nor the fact that no real fundamental distinction exists.

In the classification used in this paper the emphasis has been on the structure of the perithecium. However, it has been found that the groups of British *Nectrias* described show a close parallel to Wollenweber's classification based on the conidial states.

The following nine groups of British *Nectria* spp. have been proposed and are based chiefly on the structure of the perithecial wall.

#### **Stroma normally well developed**

*Cinnabarina* group

*Coccinea* group

*Aquifolii* group

*Ochroleuca* group

#### **Stroma reduced, absent, or replaced by a partial byssus**

*Mammoidea* group

*Episphaeria* group

*Peziza* group

*Arenula* group

*Lasionectria* group

The separation of these nine groups of British *nectrias* follows closely on the system used by Fries (1823 and 1828). Thus the first two species described by him were *Nectria* (*Sphaeria*) *coccinea* and *Nectria* (*Sphaeria*) *cinnabarina*. Although the characters given by Fries to separate these two species are not in themselves sufficient, they do represent the basic characters of the groups to which these two species belong. Under *Caespitosae*, species grouped on a stroma, Fries described *Sphaeria cinnabarina* as having rough-walled globose perithecia and *Sph. coccinea* with ovate smooth-walled perithecia. Later (1828), he described *Sph. aquifolii*, also in group *Caespitosae*, with globose perithecia becoming umbilicate-collapsed.

Under *Denudatae*, species with simple non-stromatic perithecia, Fries described *Sph. episphaeria* as having smooth, red, laterally-collapsed perithecia and *Sph. peziza* with reddish-golden, cupulate-collapsed perithecia.

These characters are expanded in the introduction to each group. It may be emphasized that these are basic characters and readily usable in the field.

One other important field character is the host relationship. On this basis *Nectria* spp. may be divided into three groups:

1. Species with a wide host range.
2. Species restricted to one or two hosts.
3. Species restricted to one specific host.

It is felt with reasonable confidence that all the British species in the first two groups are included in this paper. In the third group, collections are more

dependent on the collectors who search or work on restricted habitats. Many of the species of this group must remain to be described. Some, which have been described in early British publications but not since collected, are included in the last part of this paper under 'Incompletely known or misdetermined British Nectrias'. Others, of which there is adequate material deposited in the national herbaria, are described under their correct groups.

### ACKNOWLEDGEMENTS

In the course of the cultural studies described in this paper, very many collections have been received from British mycologists and I am greatly indebted to all those who have so kindly sent me the fresh material they have collected.

In particular I am indebted to Mr. E. W. Mason for his constant help and advice during the writing of this paper. Also to the following, who have sent me, or made available to me for examination, collections in their keeping: Mrs. F. L. Balfour-Browne, Professor C. Cappelletti, Dr. R. W. G. Dennis, Mr. H. R. Fletcher, Professor R. Heim, Professor H. J. Lam, Dr. D. P. Rogers, and Dr. R. Santesson.

The following abbreviations of collectors' names are used throughout: C.B., C. Booth; W.G.B., W. G. Bramley; E.A.E., E. A. Ellis; M.B.E., M. B. Ellis; J.E., J. Ehrlich; S.M.F., S. M. Francis; S.J.H., S. J. Hughes; E.W.M., E. W. Mason; J.W., J. Webster.

### KEY TO THE GROUPS

- A. Perithecia aggregated on a stroma
1. Perithecia globose to pomiform
    2. Perithecia, on well developed stroma, with a rough warted outer wall . . . . . CINNABARINA, p. 26
    2. Perithecia on weakly developed stroma or byssus . . . . . OCHROLEUCA, p. 34
    2. Perithecia pomiform to cupulate, outer wall covered with furfuraceous layer . . . . . AQUIFOLII, p. 6
  1. Perithecia ovoid to obpyriform, wall smooth . . . . . COCCINEA (in part), p. 42
- B. Perithecia, discrete or aggregated, without a well developed stroma
3. Outer wall covered with hairs . . . . . LASIONECTRIA, p. 100
  3. Outer wall not covered with hairs
    4. Mature perithecia mostly cupulate when dry
      5. Perithecia 250-350  $\mu$  in diameter . . . . . PEZIZA, p. 95
      5. Perithecia 150-250  $\mu$  in diameter . . . . . ARENULA, p. 98
    4. Perithecia ovoid, some with a flattened apex
      6. Perithecia 250-700  $\mu$  in diameter
        7. Perithecia with flat ostiolar disc differing in colour from rest of wall . . . . . MAMMOIDEA, p. 62
        7. Perithecia ovoid, smooth- or rough-walled on bare wood or cankered bark, not collapsed . . . . . COCCINEA (in part), p. 42
      6. Perithecia smooth-walled 100-250  $\mu$  in diameter (some associated with Sphaeriaceous fungi are larger, and show a lateral collapse when dry) . . . . . EPISPHERIA, p. 72

## THE AQUIFOLII GROUP

*Nectria aquifolii*, *N. sinopica*, *N. coryli*, *Scolecnectria cucurbitula*, *Thyronectria balsamea*, *T. lamyi*, and *T. berolinensis*.

The species in this group have slightly rough-walled perithecia, in caespitose clusters on a stroma, which undergo a pomiform collapse on drying; no marked differentiation into regions is present in the wall.

*Nectria aquifolii*, *N. coryli*, *Scolecnectria cucurbitula*, *Thyronectria balsamea*, and *T. lamyi* have ascospores forming ascoconidia in the ascus. *T. berolinensis* forms ascoconidia from the liberated ascospores and *N. sinopica* not at all. All seven species form conidia similar to the ascoconidia from short poorly developed lateral phialides on the first-formed hyphae.

The discrete yellow to yellowish red, scattered tuberculate and erumpent stromata are 500–700  $\mu$  in diameter, they arise in the phelloderm and rupture the overlying periderm. The perithecia are red, slightly darker round the somewhat papillate ostiole and appear gelatinous when young. All except *Nectria coryli* become covered with a yellowish-green furfuraceous scurf, but this is lost from older perithecia. On drying they all show a pomiform collapse irrespective of their state of development. The wall of the young perithecium, apart from two to three layers of elongated thin-walled cells lining the inner cavity, is composed of homogeneous cells continuous with the cells of the underlying stroma. However, before development is complete, the outer cells develop thick walls and lose their elasticity, then, as the perithecium increases in size, these outer layers split and peel off in flakes consisting of several cell layers together. These layers give the perithecium its furfuraceous appearance. As stated, this covering is absent in *N. coryli* and this species has a further wall characteristic. In the upper half of the mature perithecium, the central cells of the wall separate and become surrounded by mucilage which, in dried material, leaves a cavity in the centre of the wall. There is some evidence of this condition in *N. sinopica* and *N. aquifolii*, where a few cells in the centre of the wall adjacent to the ostiole separate and become mucilaginous. The condition is not related to the perithecial collapse on drying, as this is equally effective in all three species.

## CULTURAL CHARACTERS

*Thyronectria lamyi* and *T. berolinensis* have not been grown by me. In their gross appearance the cultures of the other five species are identical in the early stages. They have a sparse mycelial formation which becomes slimy following conidial production and gives a slight yellow to orange discoloration in the centre of the colony and occasionally in the agar. All except *N. sinopica* produce ascoconidia directly from the ascospores although in *T. berolinensis* they have not been observed to form from ascospores still in the ascus. These ascoconidia germinate to form hyphae. In *N. sinopica* the ascospores themselves germinate to form hyphae. In all seven species further microconidia are formed laterally from pores or poorly developed phialides on the hypae in 3 to 7 days. In *N. coryli* and *N. aquifolii* incipient sporodochial formation occurs. In *N. sinopica*, *S. cucurbitula*, and *T. balsamea* multilocular pyrenidia develop and the locules are lined with phialides.

These closely related species illustrate the situation that arises when genera

are based on a single character. In the most widely used classifications of the *Hypocreales*, genera are distinguished predominantly by the shape and septation of the ascospores. Under this system *Nectria aquifolii*, *N. coryli*, and *N. sinopica* occur in the hyalodidymae, *Scolecconectria cucurbitula* in the scolecosporae, and *Thyronectria balsamea*, *T. lamyi*, and *T. berlinensis* in the hyalodictyae. It must be realized, however, that all seven species belong to a closely related group and that only in the ascospore form do they markedly differ.

## KEY TO SPECIES

- |  |                                    |
|--|------------------------------------|
| 1. Ascospores oval to cylindrical, 1-septate . . . . .                                       | 2                                  |
| 1. Ascospores scoleco- or dictyospores . . . . .   | 4                                  |
| 2. Ascospores producing ascoconidia within the ascus . . . . .                               | 3                                  |
| 2. Ascospores not producing ascoconidia within the ascus . . . . .                           | <i>Nectria sinopica</i>            |
| 3. Perithecia with furfuraceous outer wall, ascospores $9-12 \times 3-4 \mu$ . . . . .       | <i>N. aquifolii</i>                |
| 3. Perithecia without furfuraceous outer wall, ascospores $11-13 \times 3-3.5 \mu$ . . . . . | <i>N. coryli</i>                   |
| 4. Primary ascospores scolecospores, $36-55 \times 2.5-3.5 \mu$ . . . . .                    | <i>Scolecconectria cucurbitula</i> |
| 4. Primary ascospores, dictyospores . . . . .  | 5                                  |
| 5. Ascospores forming ascoconidia in the ascus . . . . .                                     | 6                                  |
| 5. Ascospores not forming ascoconidia in the ascus . . . . .                                 | <i>Thyronectria berlinensis</i>    |
| 6. Primary ascospores, $17-26 \times 5-6 \mu$ . . . . .                                      | <i>T. balsamea</i>                 |
| 6. Primary ascospores, $15-24 \times 6-8 \mu$ . . . . .                                      | <i>T. lamyi</i>                    |

As most of these species are host-limited they can also be separated on this character.

## On Coniferous trees

- |   |                       |
|---|-----------------------|
| a. Chiefly <i>Abies</i> sp. ascospores dictyospores . . . . . | <i>T. balsamea</i>    |
| b. Other conifers, ascospores scolecospores . . . . .         | <i>S. cucurbitula</i> |

## On broad-leaved trees

- |   |                       |
|---|-----------------------|
| c. On <i>Hedera helix</i> . . . . .   | <i>N. sinopica</i>    |
| d. On <i>Ilex aquifolium</i> . . . . .                                      | <i>N. aquifolii</i>   |
| e. On <i>Ribes</i> spp. . . . .   | <i>T. berlinensis</i> |
| f. On <i>Berberis</i> spp. . . . .  | <i>T. lamyi</i>       |
| g. On broad-leaved trees, chiefly <i>Salix</i> and <i>Populus</i> . . . . . | <i>N. coryli</i>      |

*Nectria aquifolii* (Fr.) Berk., Outlines Brit. Fung., p. 393, 1860.

*Sphaeria aquifolii* Fr., Syst. Mycol., Elench., ii, p. 82, 1828.

'*Sphaeria aquifolia* Moug.' as cited by Berkeley in Smith's Engl. Fl., v, 2, p. 253, 1836.

*Nectria aquifolia* (Fr.) Berk., Outl. Brit. Fung., p. 393, 1860.

*Nectria inaurata* Berk. & Br., Ann. Mag. nat. Hist., ser. 2, xiii, p. 467-8, 1854.

*Aponectria inaurata* (Berk. & Br.) Sacc., *Michelia*, i, p. 296, 1878.

*Nectria aquifolii* (Fr.) Berk. var. *appendiculata* Feltgen, Vorstud. Pilzfl. Luxemb., iii, p. 305, 1903. Teste Höhnel, *S.B. Akad. Wiss., Wien*, I, cxv, p. 1193, 1906.

[*Nectria flavo-virens* Torrend Herb. Bresadola, on *Ilex* twigs. Teste Höhnel & Weese, *Ann. mycol. Berl.*, viii, p. 466, 1910.]

Fries (1849) recognized *Sphaeria aquifolii* as a *Nectria* but it was first transferred to this genus by Berkeley in 1860.

In 1854 Berkeley and Broome published the name *Nectria inaurata* based on a collection by Currey on holly. They did not appreciate that the ascospores of *N. aquifolii* produced ascoconidia, and mature specimens of this species with asci full of ascoconidia were referred to *N. inaurata*. Currey (1855) stated that

in his opinion the collection cited by Berkeley and Broom was *N. sinopica*. The author agrees with Tulasne who stated that it was *N. aquifolii*.

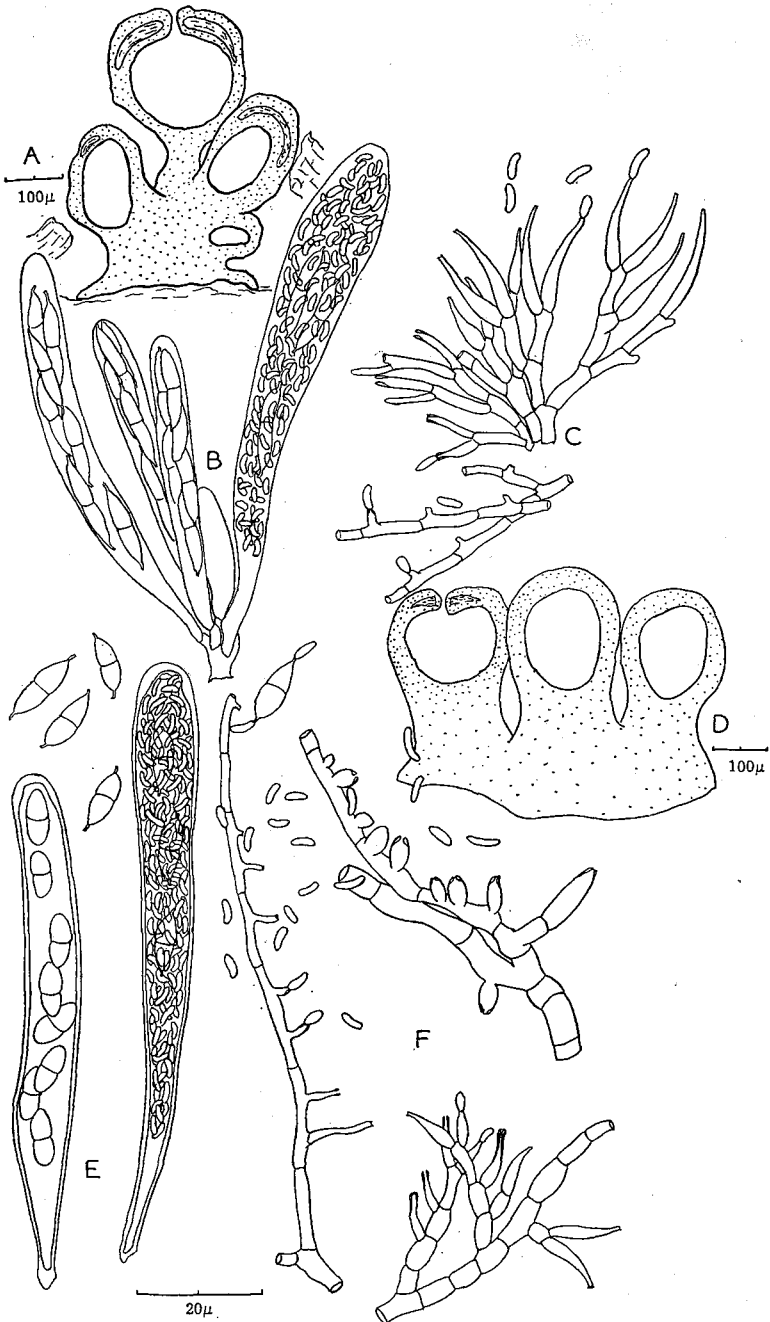


FIG. 1. *Nectria coryli*. A, diagrammatic section of perithecia and stroma; B, asci with ascospores and ascoconidia; C, conidiophores and conidia, lower figure shows primary conidiophores. *Nectria aquifolii*. D, diagrammatic section of perithecia and stroma; E, asci with ascospores and ascoconidia; F, primary and secondary conidiophores and conidia.



Currey (1858) first figured the asci and ascospores from an authentic collection of *Nectria aquifolii* sent by Fries to Mougeot but he did not mention the ascoconidia, these were first figured in 1865 by Janowitsch and independently in the same year by Tulasne.

#### DESCRIPTION

Perithecia clustered on an erumpent yellow to red tuberculate stroma 500–700  $\mu$  in diameter. They are globose, red becoming darker around the papillate ostiole. When mature they are covered with a greenish-yellow furfuraceous scurf and measure 270–330  $\mu$  in diameter, but on drying shrink and undergo a pomiform collapse. The lateral wall is 24–28  $\mu$  wide with cells 11–16  $\times$  7–8  $\mu$ , the cells of the outer wall are homogeneous with the cells of the stroma and the only zonation shown is 2–4 layers of elongated and very thin-walled cells that line the locule. As the perithecium matures, the cell walls in the outer 3–4 layers thicken; then as the perithecium increases in size these cells flake off to give the furfuraceous covering to the outer wall. Some perithecia show a separation and gelatinization of some of the cells in the middle of the wall at either side of the ostiole, a condition which is more marked in *Nectria coryli*.

The asci are cylindrical-clavate, and at the stage when they have eight distichous ascospores measure 70–80  $\times$  6–7  $\mu$  but after they have become filled with ascoconidia they measure 90–100  $\times$  8–9  $\mu$ . The ascospores are broadly fusoid with a single central septum and measure 9–12  $\times$  3–5  $\mu$ . When they are mature a small phialide develops at either end of the spore and from these are produced the ascoconidia which are hyaline, allantoid, 3.5–4.5  $\times$  1  $\mu$ . The ascoconidia entirely fill the lumen of the ascus and the ascospores remain as empty sacs.

#### CULTURES

Ascospores do not germinate directly but form ascoconidia from terminal pores; this occurs even when ascospores are placed on agar in an immature condition. Ascoconidia germinate readily and form a hypha from each end. The initial mycelium is 1.5–2  $\mu$  wide and forms a sparse felt which covers the surface of the agar in a test-tube in about 14 days. Short lateral phialides develop on this mycelium in 4–7 days, these are 7–10  $\mu$  long and 2  $\mu$  wide at the base. Conidia are produced in abundance and give the colony a slimy appearance. These conidia are hyaline, cylindrical with rounded ends, and measure 3–4  $\times$  1–1.5  $\mu$ . On 2 per cent. potato dextrose or malt agar in light, the colony is first colourless. In about 7 days it develops a marked yellow stain which in the centre becomes gradually orange. This orange colour finally covers the whole surface.

In 10–12 weeks discrete stromata develop on the surface of the agar and perithecia form on the surface of these. Mature asci were found after 16 weeks.

#### SPECIMENS EXAMINED

Exsiccata ex Herb. R.B.G. Kew

Mougeot & Nestler, Stirpes cryptogamicæ, No. 879 (1826); *Sphaeria aquifolii* on *Ilex aquifolia*. (Two parts, authentic for name.)

Cooke, M. C. Fungi Brit. No. 259 (1866); *Nectria aquifolia*, No. 476 (1875-9);  
*Nectria inaurata* Berk. & Br.

Jaap, O. Fungi Selecti, No. 53 (1904); *Nectria inaurata* Berk. & Br.

Libert, M. A. Pl. Crypt. Arduennae Fasc. ii, No. 146 (1832); *Sphaeria aquifolii*  
 (2 pts).

Rabenhorst, Fungi Europaei, No. 46 (1859); *Nectria inaurata* Berk. & Br.

Roumeguère, C. Fungi Selecti Gallici, No. 484 (1879); *Sphaeria aquifolii*.

Sydow, H. Mycotheca germanica, No. 2138 (1924); *Nectria aquifolii* (Fr.) Berk.

Vize, J. E. Micro fungi Brit. No. 374 (1882); *Nectria inaurata* Berk. & Br.

*Nectria aquifolia* folder Herb. B.M. Nat. Hist.

Libert, M. A. Pl. Crypt. Ard. Fasc. ii, No. 146 (1832), *Sphaeria aquifolii*.

Mougeot & Nestler's, Stirp. Crypt. No. 879 (1826), *Sphaeria aquifolii*.

*Oponectria* folder Herb. B.M. Nat. Hist.

Rabenhorst, Fungi Europaei No. 46 (1859), *Nectria inaurata* Berk. & Br. on *Ilex*,  
 Marshfield, Gloucestershire, G. E. Broome (authentic).

*Nectria aquifolii* folder Herb. I.M.I.

On *Ilex*. Haslemere, Surrey, E.W.M., Sept. 52 (22780); Burnsall, Yorks.,  
 E.W.M., Oct. 43 (22779); Kingthorpe Woods, Yorks., S.J.H., April 46 (4932);  
 Ranmore Common, Surrey, S.J.H., June 46 (5962); Pickering, Yorks., W.G.B.,  
 Dec. 56 (68040a); Jan. 57 (68153); Ranmore Common, Surrey, C.B., Mar. 58  
 (72631, 72172).

Herb. I.M.I. Ex Herb. Ehrlich

*Sphaeria aquifolii* Fr. Moug. 278 (ex Herb. Uppsala, slide only, ex Type coll.  
 teste Ehrlich). On *Ilex*, Ranmore Common, Surrey, J.E., Sept. 34 (22782);  
 Norwich, Norfolk, E.W.M., Oct. 34 (22783); Burnham Beeches, Bucks, J.E.,  
 Oct. 34 (22781); Dublin, Eire, P. O'Connor, May 35 (51658).

Exsiccata published as *Nectria aquifolii* and found to be *N. punicea*.

Kryptogamae exsiccatae, Mus. malat. Vindobon, No. 1610; *Nectria aquifolii*.

Vize, J. E. Microfungi Britannica, No. 373; *Nectria aquifolia*.

Roumeguère Fungi Gallici, No. 2181; *Nectria aquifolia*.

*Nectria coryli* Fuckel, Fung. Rhen. Exs., Suppl. 1, No. 1582, 1865 and Symb.  
 Myc., p. 180, 1870.

*Nectria coryli* f. *salicis* Rehm, Asc. Exs. 14, No. 680, 1882; *Hedwigia*, xxii, p. 54,  
 1883.

*Chilonectria coryli* (Fuckel) Ellis & Everh., North Amer. Pyrenom., p. 117, 1892.

*Creonectria coryli* (Fuckel) Seaver, *Mycologia*, 1, p. 186, 1909.

*Coelosphaeria acervata* Karsten, *Medd. Soc. Fauna Fl. Fenn.*, add vi, p. 41, 1879,  
 teste Karsten *Acta Soc. Fauna Fl. fenn.*, ii, 6, p. 12, 1885.

*Nectria coryli* and *Scoleconectria* [*Nectria*] *cucurbitula* have been the subject  
 of much confusion especially in earlier writings. They are now separated by the  
 fact that *Scoleconectria cucurbitula* has scolecospores and occurs only on conifers.  
*N. coryli* occurs on many deciduous trees excluding *Ilex* and has didymospores.  
 The part of Fries' Seler. Suec. No. 183 *N. coccinea* in Herb. R.B.G. Kew, ex  
 Herb. Berk. is in fact *N. coryli*.

Weese (1914) stated that *Calonectria aurigera* (Berk. & Rav.) Sacc. is the same  
 species as *Nectria coryli*. Weese was examining an exsiccatum by Ellis (Fungi

## STUDIES OF PYRENOAMYCETES: IV

Nova Caes. No. 69 on *Chionanthus*) which is a misdetermination. Examined of Berkeley and Ravenel's collection of *N. aurigera* on *Fraxinus*, Santa Cruz S.C., in Herb. R.B.G. shows it to be a *Calonectria* species.

### DESCRIPTION

Perithecia clustered on an erumpent tuberculate stroma are globose, without an ostiolar papilla, red becoming darker in colour and measure 290–350  $\mu$  in diameter. They show a pomiform collapse on drying when they shrink to 240–260  $\mu$  in diameter. The wall is 45–55  $\mu$  thick and composed of cells 8–10  $\times$  5–8  $\mu$ . These are homogeneous with the cells of the stroma in the young perithecium, but the outer 2–3 layers of cells have a thickening of their outer walls at maturity. No separation or flaking of these cells has been seen and hence no furfuraceous covering is present. A marked characteristic of this species is the gelatinization of the central region of the wall in the upper half of the mature perithecium, here the cells separate as their walls become gelatinous.

The asci are clavate with a thin wall and eight distichous ascospores; at this stage they measure 60–65  $\times$  6–8  $\mu$ . The ascospores are not discharged but develop a pore at each end and these phialides form ascoconidia until the lumen of the ascus is full and the ascus enlarges to 75–100  $\times$  9–12  $\mu$ . The ascospores are broadly fusoid and measure 11–13  $\times$  3–3.5  $\mu$ , by the time ascoconidial production is complete they are devoid of contents. The ascoconidia are allantoid, hyaline, and measure 3–5  $\times$  1–1.5  $\mu$ . The surface of the developing stroma before the initiation of perithecia is covered with hyaline fusoid conidia 3–6  $\times$  1.5–2  $\mu$  which develop from short phialides.

### CULTURES

Ascospores do not germinate directly, but produce ascoconidia which germinate to form a hypha at one or both ends. Growth on potato dextrose agar at 24° C. extends about 3 cm. along the slant after 10 days. The colony is composed of a sparse hyaline mycelium which is accompanied below with a slight yellow and later yellowish-brown discoloration of the agar. Allantoid, hyaline conidia 3.5–6  $\times$  1–1.5  $\mu$  are formed from poorly differentiated lateral phialides along the hypha and as these conidia accumulate in large numbers, the surface of the colony appears slimy and finally orange in colour. In older cultures the phialides form as terminations to dichotomously branched conidiophores and aggregations of these conidiophores form a loose synemma or pseudostroma. No perithecia developed in my agar cultures.

### SPECIMENS EXAMINED

*Nectria coryli* folder Herb. R.B.G. Kew

Fuckel, Fungi Rhen. No. 1582 (1865), *Nectria coryli* (type coll.); Rehm, Ascomyceten No. 231 (1874), *N. coryli* Fuckel; Rehm, Ascomyceten No. 680 (1882), *N. coryli* Fuckel f. *salicis* Rehm; Sydow, Mycotheca Marchica No. 1151 (1886), *N. coryli* Fuckel f. *salicis* Rehm; Rehm, Ascomyceten No. 526 (1879), *N. coryli* Fuckel f. *populi* Rehm; Saccardo, Mycotheca veneta No. 1446 (1881), *Aponectria inaurata* (Berk. & Br.) Sacc.; Fries, Scler. Suec. No. 183 (1821), *Sphaeria coccinea* (pro parte Herb. R.B.G. Kew).

## Other collections

On *Salix*, Marishes, Yorks., W.G.B., Jan. 57 (I.M.I. 68257). This collection was the only one obtained in a fresh condition and suitable for culturing.

*Nectria sinopica* Fries, Sum. Veg. Scand., ii, p. 388, 1849.

*Sphaeria sinopica* Fries, Syst. Mycol., Elench., ii, p. 81, 1828.

*Nectria inconspicua* Berl. (non Starb.) Herb. Mus. Bot. Berl., teste Weese, *S.B. Akad. Wiss., Wien*, 1, cxxv, p. 526, 1916.

## Stat. conid.

*Sphaeria mougeotii* Fr., Elench. Fung., ii, p. 100, 1828.

*Sphaeronema hederæ* Fuckel, Fung. Rhen. Exs. viii, No. 775, 1863, and Symb. Myc., p. 178, 1870.

*Sphaeronaemella mougeotii* (Fr.) Sacc., *Syll. Fung.*, iii, p. 617, 1884.

*Zythia mougeotii* (Fr.) Jaczewsky, *Novv. Mem. Soc. Nat., Moscow*, xv [xx], pp. 367-8, 1898.

*Zythiostroma mougeotii* (Fr.) Höhn., *Mitt. bot. Lab. tech. Hochsch., Wien*, viii, pp. 88-90, 1931.

This species strongly resembles *Nectria aquifolii* but differs in habitat, very slightly in ascospore size, and in absence of ascoconidial production within the ascus.

## DESCRIPTION

Perithecial development is usually preceded by the formation of pycnidia. These form in the cortex although the overlying periderm is usually split off by the time they are mature. They may also form on the perithecial stroma, either in the early stages of its development or accompanying the perithecia. They are 350-500  $\mu$  in diameter and 450-500  $\mu$  high; globose, red, and slightly darker round the apical pore which measures 100-150  $\mu$  in diameter. On drying they show a pinched collapse and the apical pore forms a slit. The upper wall is 30-45  $\mu$  thick and formed of thick-walled cells 6-7  $\mu$  in diameter; the lower wall in contact with the host is poorly developed and without thick-walled cells. Convolution of this wall form folds of tissue that project into the cavity of the pycnidium, thereby increasing the inner wall area and in consequence the number of phialides. The phialides are flask-shaped 8-10  $\times$  2  $\mu$  at the base. Conidia are fusoid to allantoid 2-3  $\times$  1  $\mu$ .

The perithecial stromata extend along the branches of recently cut ivy. They are dispersed, yellow to red, tuberculate, finally erumpent and 500-700  $\mu$ , in diameter. The globose perithecia are crowded on the surface of the stroma and appear gelatinous and light red when young, but become darker with age and finally may be covered with a yellowish-green furfuraceous scurf. They measure 250-300  $\mu$  in diameter when moist but on drying shrink to 140-170  $\mu$  in diameter and show a pomiform collapse. The wall is 40-65  $\mu$  thick; in the early stages of development the wall cells are continuous and homogeneous with the cells of the stroma. As development proceeds, three wall regions become apparent. The outer region is formed of the outer two to three layers of cells which develop thick walls and become yellow, globose 6-9  $\mu$  in diameter or elongated 8-12  $\times$  6-7  $\mu$ . The central region measures 25-35  $\mu$  and has cells which remain un-

differentiated  $8-10 \times 6-8 \mu$ . As the locule of the perithecium forms, it is lined by several layers of elongated cells with very thin walls; these cells become compressed during the later stages of development. Copious periphyses form below the ostiole and in the upper quarter of the perithecium, the remainder of the inner wall is covered by the asci.

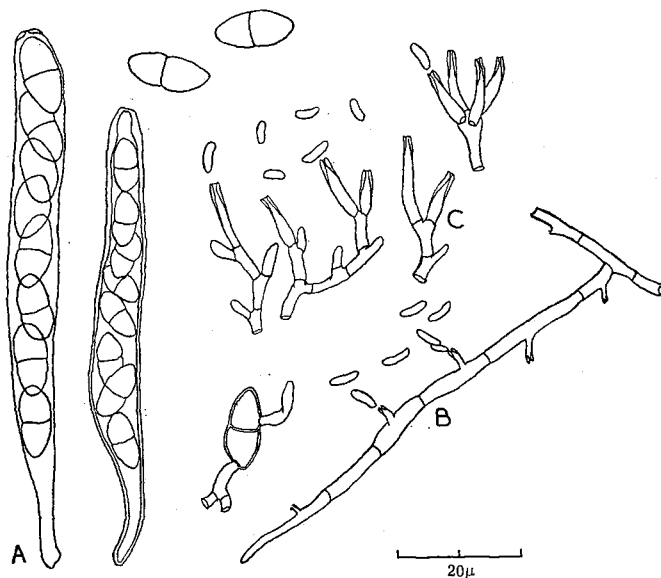


FIG. 2. *Nectria sinopica*. A, asci and ascospores; B, microconidia and conidiophores; C, pycnospores and phialides from pycnidium.

The asci are cylindrical with a rounded thickened apex and eight monostichous to obliquely monostichous ascospores, and measure  $55-70 \times 6-8 \mu$ .

Ascospores are smooth hyaline, broadly elliptical with a single central septum; they measure  $9-12 \times 4-6 \mu$ .

#### CULTURES

Ascospores germinate readily, but growth is slow and aerial mycelium  $1-1.5 \mu$  wide forms sparsely on potato dextrose and potato carrot agar. The superficial hyphae form poorly differentiated lateral phialides up to  $10 \mu$  long in 4-8 days, these produce hyaline, allantoid conidia  $4-8 \times 1-1.5 \mu$ . These conidia give the culture a yellow to orange colour and slimy appearance. Pycnidia begin to develop in culture in 5-6 weeks and finally measure  $400-500 \mu$  in diameter and  $450-550 \mu$  high with phialides  $6-10 \times 1-1.5 \mu$ ; pycnospores are hyaline, fusoid,  $3-4 \times 1-1.5 \mu$ . (The pycnidial wall is evenly developed, invagination occurring all round the inner wall, whereas, under natural conditions, invagination is confined to the base and the upper part of the wall is thickened.)

#### *Type habitat*

On dead bark and on the wood of recently cut but still firm stems and adventitious roots of *Hedera helix* L.

Herb. Uppsala *Sphaeria sinopica* Fr. (Scripsit Fries) Scania, Lund in H.Bot. (authentic for name, teste Ehrlich, slide in Herb. I.M.I.).

This species is restricted to one host and has been recorded for most countries in Europe. It was first recorded for Britain by Berkeley (1838).

#### SPECIMENS EXAMINED

*Nectria sinopica* folder Herb. R.B.G. Kew

Cooke, Fung. Brit. Exs., ed. 1, No. 664 (1865-71); ed. 2, No. 477 (1875-9). Plowright, Sphaer. Brit. 1, No. 9 (1873). Desm., Pl. Crypt. Fr. ed. 1, xxvi, No. 1259 (1843), sub. *Sphaeria sinopica*; Moug. & Nestl., Stirp. Crypt. Vog.-Rhen. xiv, No. 1335 (1854), sub. *Sph. sinopica*; De Not. Erb. Critt. Ital. No. 493; Fuckel, Fung. Rhen. Exs. viii, no. 775 (1863), sub. *Sphaeronema hederæ*; Suppl. vi, No. 2051 (1867), sub. *Nectria sinopica*. Thümen, Myc. Univ. iii, No. 271 (1875), (Leg. Plowright, King's Lynn, Norfolk). Kunze, Fungi Sel. Exs. iv, No. 343 (1880). Sacc. Myc. Ven. xv, No. 1483 (1881). Roumeguère, Fungi Gall. Exs. iv, No. 372 (1879). Rehm, Asc. Exs. xviii, No. 878 (1886). Sydow, Myc. Germ. xxxix, No. 1930 (1923).

*Nectria sinopica* folder in Herb. I.M.I.

On *Hedera*, Egham, Surrey, Miss Notley, Jan. 43 (9766); Stradey Woods, Llanelly, M.B.E., Aug. 46 (6666); Mulgrave Woods, Yorks., M.B.E., Sept. 46 (7475); Stepsbridge, Devon, S.J.H., Sept. 47 (19096); Mulgrave Wood, Yorks., C.B., Sept. (53560); Petworth, Sussex, S. Holman, Nov. 55 (71244); Pickering, Yorks., W.G.B., Mar. 56 (62651 and 62652); Presteign, Radnorshire, J. M. Dingley, Sept. 57 (71245).

Herb. I.M.I. Ex Herb. Ehrlich

Ranmore Common, Surrey, E.W.M. and J.E., Sept. 34 (22847); Droitwich, Worcs., J.E. and C. G. C. Chesters, Nov. 34 (22848); Birmingham, Warwicks, C. G. C. Chesters, Jan. 35 (52222); Surlingham, Norfolk, E.A.E., Jan. 35 (52221).

#### A DISSERTATION ON THE GENERA OPHIONECTRIA AND SCOLECONNECTRIA

*Ophionectria* is separated from *Scoleconnectria* by the absence of a stroma and from *Calonectria* by a length: breadth ratio of the ascospores of more than 10:1 which in the young ascus are parallel and of equal length. It is distinguished from *Podonectria* and *Tubeufia* by the absence of bituncate asci and pseudoparaphyses. Although the ascospores are more than ten times as long as broad in *Ophionectria* they are not filiform in the sense of thread-like.

The genus *Ophionectria* was proposed by Saccardo (1878) who gave the following diagnosis: Perithecia Nectriae-Asci octo-spori. Sporidia filiformia multiseptata v. multiguttulata. Three species were included in the following order:

*Ophionectria trichospora* (Berk. & Br.) Sacc.

*Ophionectria mellina* (Mont.) Sacc.

*Ophionectria paludosa* (Crouan) Sacc.

*Ophionectria trichospora* was taken as the type of the genus by Seaver (1909) and Höhnel (1912). This is undoubtedly the best choice as *O. mellina* was transferred to *Calonectria* by Höhnel and Weese (1910) and the perithecia of *O. paludosa* were described as 'albo-carnea', whereas in Saccardo's diagnosis of the genus *Ophionectria* they are described as being nectrioid.

Since 1898 the genus has become a depository for unrelated species which have merely filiform ascospores in common. The following British species recorded as *Ophionectria* serve in part to exemplify the heterogeneous nature of this genus: *Ophionectria cylindrospora*, *O. cerea*, and *O. paludosa*.

The first species has nectrioid perithecia developing on a stroma with 2-4 spored asci; the ascospores do not germinate directly but form ascoconidia within the ascus. Conidia are formed from short lateral phialides on the superficial mycelium and later in pycnidia. *Ophionectria cerea* and the species for which the name *O. paludosa* was used in Britain are closely related to each other but differ from *O. cylindrospora* in having perithecia and asci resembling the ascocarps of the *Pseudosphaeriales*. Growth in culture is slow and the only conidia formed are of the form genus *Helicosporium*.

*Ophionectria trichospora*, the type species of the genus, has solitary non-stromatic perithecia, unitunicate asci, and ascospores that do not form ascoconidia in the ascus.

In this paper it is proposed to follow Seaver (1909) in placing *Ophionectria cylindrospora* in the genus *Scoleconectria*. This genus was erected by him for *Ophionectria*-like species with perithecia seated on a stroma; he gave the type species as *O. scolecospora* Bref. After examining Seaver's material I consider this latter species to be identical with *O. cylindrospora* (Sollm.) Berl. & Vogl. However, *Scoleconectria cucurbitula* (Tode ex Fr.) Booth provides an earlier name than either *O. cylindrospora* or *O. scolecospora* for this species and it is therefore used here.

*Ophionectria paludosa* was recorded for this country by Petch (1944) from a collection by Mr. E. A. Ellis. On examination, this collection was found to be identical with *Tubeufia helicomyces* Höhnel and, as it is obviously co-generic with the original species of *Tubeufia*, this genus is used for both this species and *O. cerea*.

Petch (in litt. 1944) stated that he had taken up the name *Ophionectria paludosa* from Saccardo's description. There is no material of this species listed in Saccardo's Herbarium and I have been unable to visit Finistère to see Crouan's material. If these two are the same species then *paludosa* is the earlier epithet.

A description of *Scoleconectria cucurbitula*, *Thyronectria balsamea*, and *T. lamyi* is now given. Their relationship to the *Aquifolii* Nectrias has been discussed on p. 6.

***Scoleconectria cucurbitula* (Tode ex Fr.) Booth, comb. nov.**

*Nectria cucurbitula* (Tode ex Fr.) Fries, Summa Veg. Scand., ii, p. 388, 1849.

*Sphaeria cucurbitula* Tode, Fung. Meekl., ii, p. 38, 1791.

*Sphaeria cucurbitula* Tode ex Fr., Syst. Mycol., ii, p. 415, 1823. Vide Fr. Scler.

Suec., viii, p. 263, 1822.

*Nectria cylindrospora* Sollm., Bot. Ztg., xxii, p. 265, 1864.

*Ophionectria cylindrospora* (Sollm.) Berl. & Vogl., in Sacc., Syll. Fung., xi, p. 995, 1891.

- Nectria rosellinii* Carestia, in Rabenh., Fung. Europ. Exs. No. 923, 1866.  
*Chilonectria rosellinii* (Carestia) Sacc., *Michelia*, 1, p. 280, 1878.  
*Ophionectria scolecospora* Bref. & Tavel in Brefeld, Unters, Gesamtg. Myk., x, p. 178, 1891.  
*Scoleconectria scolecospora* (Bref. & Tav.) Seaver, *Mycologia*, 1, p. 198, 1909.  
*Zythia pinastri* Karsten, *Rev. Mycol.*, vii, p. 106, 1885.  
*Zythiostroma pinastri* (Karsten) Höhnelt apud Weese, *Mitt. bot. Lab. Tech. Hochsch. Wien*, viii, p. 90, 1931.

*Sphaeria cucurbitula* was first described by Tode (1791) loc. cit. In his figures, the collapsed cupulate perithecia with rough walls are clearly shown (these are not features of *Nectria cucurbitula* sensu Fuckel). Tode did not mention the host, but Albertini & Schweinitz (1905) said that this species was frequent on conifers.

The species was included by Fries (1823), in his 'Systema' citing his exsiccatum Scler. Suec. No. 263 as authentic. The first British record was in fact a misdetermination by Berkeley, who cited it as occurring on small dead shoots of ash: this collection is *Nectria cinnabarina*. Berkeley and Broome (1851) stated: '*Sph. cucurbitula* Tode is easily distinguished from all other similarly coloured species by its asci being filled with numerous minute curved sporidia.' Currey's figure (1859) of *N. cucurbitula* was in fact *N. coryli*.

As no Tode material of *Sph. cucurbitula* is known to exist, and as Fries' Scler. Suec. 236 *Sph. cucurbitula* agrees with Tode's figures, part of this exsiccatum cited below in Herb. R.B.G. Kew is taken as lectotype of the species.

Table showing the writer's determinations of *Sph. cucurbitula* Fries 263

Label	Herbarium	Substratum	Determination
<i>S. cucurbitula</i>	Kew	Bark and leaf scars, conifers	<i>Scol. cucurbitula</i>
<i>S. cucurbitula</i> Tod.	Kew <sup>1</sup>	"	<i>Scol. cucurbitula</i>
<i>S. cucurbitula</i> Tod.	Brit. Mus.	"	<i>Scol. cucurbitula</i>
<i>S. cucurbitula</i> Tod.	Edinb.	"	<i>Scol. cucurbitula</i>
<i>S. cucurbitula</i> Tod.	Uppsala	"	<i>Scol. cucurbitula</i>

<sup>1</sup> Lectotype marked in Herb. Kew.

Fuckel (1870) restricted the species to coniferous hosts but neither his description nor his exsiccatum Fung. Rhen. 893, which is cited as authentic, agree with Tode's description or figures of *Sphaeria* (*Nectria*) *cucurbitula*. Unfortunately, it is Fuckel's concept of the species that has been generally adopted in Europe. As this cannot be accepted, Fuckel's collection is renamed *Nectria fuckeliana*, p. 56.

The relationship between the perithecia and pycnidia was first demonstrated by Brefeld and Tavel (1891) when the pycnidia developed in ascospore isolations of the *Scoleconectria*.

#### DESCRIPTION

The perithecia are crowded on an erumpent stroma that arises in the cortex and ruptures the overlying periderm. This stroma is pseudoparenchymatous and formed of homogeneous thin-walled cells 10-18 × 8-10 μ.

Perithecia are globose to pomiform with a rather rough wall that may be



covered with a green furfuraceous scurf. They measure  $250\text{--}400\ \mu$  in diameter and on drying show a cupulate collapse. In section, the wall is  $70\text{--}80\ \mu$  thick, and, apart from the 3-4 layers of very thin-walled cells lining the perithecial cavity, no marked differentiation into layers is present. The outer wall is formed of globose cells  $9\text{--}11\ \mu$  in diameter interspersed with hexagonal cells  $10\text{--}14 \times 5\text{--}9\ \mu$ . These gradually merge into the more elongate cells of the inner layers which measure  $8\text{--}14 \times 3\text{--}4\ \mu$ .

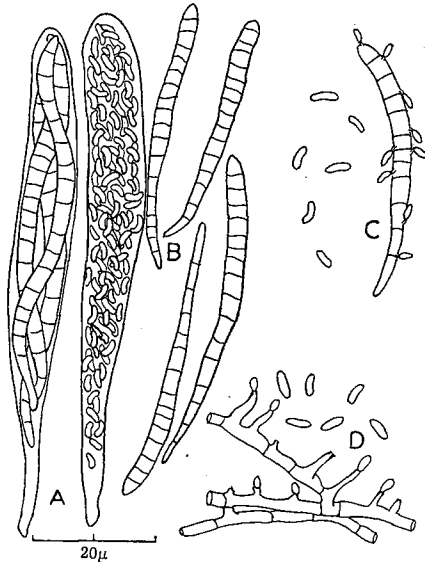


FIG. 3. *Scoleconectria cucurbitula*. A, asci with ascospores and ascoconidia; B, ascospores; C, ascospore forming ascoconidia; D, conidia and conidiophores from young culture.

The asci are cylindrical to clavate with a rounded apex and measure  $60\text{--}75 \times 7\text{--}9\ \mu$  with up to four ascospores; when full of ascoconidia the asci increase to  $75\text{--}95 \times 8\text{--}10\ \mu$ .

The ascospores are hyaline, narrowly clavate, and tapering towards the base. They have 14-18 irregular transverse septa and measure  $36\text{--}55 \times 2.5\text{--}3.5\ \mu$ . Ascospores are not discharged directly, but produce ascoconidia from small terminal pores whilst still within the ascus, until the whole lumen of the ascus is filled and the ascospores disintegrate. The ascoconidia are hyaline, allantoid, and  $3\text{--}4.5 \times 1\ \mu$ .

*Scoleconectria cucurbitula* has a *Zythiostroma* pycnidial state. These pycnidia occur in a similar position to and generally before the perithecia and are often associated with the latter in the early stages of perithecial development. Pycnidia may also occur on bare wood, in which case there is no appreciable stroma formation below. They resemble the perithecia in colour, but have a more irregular globose shape, a larger ostiole, and measure  $250\text{--}400\ \mu$  in diameter with a wall  $30\text{--}43\ \mu$  thick. The wall cells are globose to elongated with a wide variation in size. When elongated they measure  $6\text{--}19 \times 8\ \mu$ , and when globose  $6\text{--}8\ \mu$  in diameter. The inner wall shows convolutions that increase the inner surface area, the whole of which is covered by phialides; these are  $6\text{--}8 \times 2\ \mu$  at the base and narrowing towards the apex. Conidia produced from these fill the

lumen of the pycnidium and are hyaline, yellow to orange in mass, allantoid, and  $4-6 \times 1 \mu$ .

#### CULTURES

The initial mycelium is sparse, hyaline, with hyphae  $1.5 \mu$  wide; however, thicker hyphae  $2-3 \mu$  wide soon develop. Short lateral phialides form on these hyphae in 2-3 days on 2 per cent. malt or potato dextrose agar at  $22^\circ \text{C}$ . These phialides resemble short pegs and are  $2-3 \mu$  wide at the base. The masses of conidia formed from these give the young colony a slimy appearance, the conidia are orange in mass, cylindrical to allantoid,  $3-8 \times 1-1.5 \mu$ . No marked discoloration of the agar occurs.

In 2-3 weeks the superficial hyphae form white floccose pustules and below these loose pseudoparenchymatic stromata develop. Pycnidia begin to form on the surface of these in 5-7 weeks, they are irregularly globose with a convoluted inner wall. The wall is  $26-35 \mu$  thick and formed of 5-6 layers of cells. In the outer layers the cells are globose  $12-16 \times 6-8 \mu$ . The inner layers have progressively smaller cells until those giving rise to the phialides are  $3-4 \times 2-3 \mu$ . Phialides develop directly from these inner cells or occur as terminations to short-branched conidiophores. They are narrowly subulate, densely crowded over the inner wall of the pycnidium, and measure  $8-14 \times 1-2 \mu$  at the base and  $1 \mu$  at the apex. Pycnosporos are hyaline but orange in mass, cylindrical to allantoid,  $3-4 \times 1-1.5 \mu$ .

Conidiophores may also form on the surface of the stroma where this is not covered by the formation of pycnidia.

#### SPECIMENS EXAMINED

*Ophionectria cylindrospora* folder Herb. R.B.G. Kew

On *Abies balsamea*, New Brunswick, Canada, J.E., Dec. 1930.

*Ophionectria scolecospora* folder Herb. R.B.G. Kew

On *Pinus strobus*, Newfield, New Jersey, J. B. Ellis, 1886. Otto Jaap, Fungi selecti exsiccati, No. 54 (1904).

*Chilonectria cucurbitula* folder Herb. R.B.G. Kew

J. B. Ellis, Fungi of New Jersey, U.S.A. No. 3083, sub. *Nectria cucurbitula*. Rabenhorst, Fungi Europaei No. 923 (1866), sub. *N. rosellinii* Carest.

*Nectria cucurbitula* folders Herb. R.B.G. Kew

Ellis & Everhart, North Amer. Fungi, No. 1551 (1886), *Nectria cucurbitula*. Fries, Scler. Suec. No. 263 (1822), *S.[phaeria] cucurbitula* Tode (2 parts). ex Herb. Berk. 4688 *Sph. cucurbitula*, N. Jersey. Klotzsch, Herb. Mycol. 248, *N. cucurbitula*. J. W. Ellis, *N. cucurbitula*, Tode, Bridston, G.B., 1911.

*Scoleconectria scolecospora* folders Herb. New York Botanical Garden, U.S.A.

Ellis & Everhart, North American Fungi, No. 1551 (1886), sub. *Nectria cucurbitula*. C. F. Baker, Pacific Slope Fungi, No. 68, *Ophionectria scolecospora*; Ellis & Everhart, Fungi Columbiani cont. C. L. Shear No. 1433, *Chilonectria cucurbitula* (Tode) Sacc. On *Pinus*, Durham, N. Carolina det. F. J. Seaver 1937; Beaverkill, New York, Aug. 1938, confirmed F. J. Seaver.

*Scolecnectria cucurbitula* folder Herb. I.M.I.

On *Pinus strobus*, Bagshot, Surrey, J. W. Munroe, Feb. 24 (18528). On *P. sylvestris*, Wishanger, nr. Churt., Surrey, S. Batko, April 55 (59874). On *P. strobus*, Exs. Fungi Columbiani 4770 (18533) *Scolecnectria scolecospora* (Bref.) Seav., Ont., Canada, J. Dearness.

*Conidial*

On *Pinus nigra*. Petrak, Mycotheca generalis, 2100, *Zythiostroma pinastris* (Karst.) Höhnel (33503). On *P. sylvestris*, nr. Cambridge, J. Rishbeth, Aug. 56 (63519). On *Pinus* sp. nr. Brandon, Sussex, J. Rishbeth, Jan. 57 (68124a).

Herb. I.M.I. Ex Herb. Ehrlich

On *Abies balsamea*. Alma, N.B., Canada, J.E., Sept. 30 (52267); Bear Island, Ontario, G. D. Darker, June 26 (52276); Gagetown, N.B., Canada, R. E. Balch, Nov. 34 (52277); on *A. grandis*, nr. Corvallis, Oregon, N. L. Gooding, Dec. 29 (52281); on *Pinus strobus*, New Hampshire, U.S.A., A. G. Kevorkian, Sept. 32 (52269); on *P. sylvestris*, Windsor Park, Berks., J.E., April 35 (18527).

### THYRONECTRIA AND PLEONECTRIA

British authors have used the name *Pleonectria* in connexion with the two doubtfully British species which have muriform ascospores. These are *Pleonectria berlinensis* and *P. lamyi*.

Seeler (1940), in his monographic study of the genus *Thyronectria*, followed Seaver (1909) in treating *Pleonectria* as a synonym of *Thyronectria*. This latter genus was erected by Saccardo (1875) to include all *Nectria*-like species with muriform ascospores. In the following year he split the genus, retaining *Thyronectria* for species with perithecia immersed in a stroma with the type species *T. patavina*. Those species with discrete or caespitose perithecia seated on a stroma were placed in the genus *Pleonectria* with *P. lamyi* as the type. Saccardo stated that *Pleonectria* differed from *Thyronectria* almost as *Cucurbitaria* from *Thyridium*.

Seaver (1909) and Seeler (1940) found the stromatic character insufficient justification for erecting the genus *Pleonectria*, especially as they were able to ascertain from the Saccardo figures that the perithecia of *Thyronectria patavina* were not immersed completely. In this paper it is proposed to use the genus *Thyronectria* and to consider *Pleonectria* as a synonym.

Following Seeler, *Thyronectria balsamea* is also placed here. All three species are doubtfully British, but all have been recorded in Europe and frequently in North America.

They all show a close similarity in perithecial structure, and all form ascogonia, although in *Thyronectria berlinensis* they are only found after the ascospores have been liberated from the ascus. In *T. lamyi* and *T. balsamea*, secondary or macroconidia are formed in pycnidia on a stroma, but in *T. berlinensis* they are formed on a sporodochial stroma. In all three they are usually succeeded by perithecia on the same stroma.

***Thyronectria balsamea*** (Cooke & Peck) Seeler, *J. Arnold Arbor.*, xxi, p. 442, 1940.

*Scolecnectria balsamea* (Cooke & Peck) Seaver, *Mycologia*, i, p. 200, 1909.

*Nectria balsamea* Cooke & Peck in Cooke, *Grevillea*, xii, p. 81, 1884, et nomen in Peck, *N. York State Mus. Ann. Rept.* xxvi, p. 81, 1874.

*Calonectria balsamea* (Cooke & Peck) Sacc. *Syll. Fung.*, ix, p. 986, 1891.

*Pleonectria pinicola* Kirschstein, *Abh. Bot. Ver. Prov. Brandenburg*, xlviii, p. 59, 1906. (Teste Ehrlich in litt.)

*Ophionectria cylindrospora* (Sollm.) Berl. & Vogl. var. *tetraspora* Weese, *Zbl. Bakt.*, 2 Abt. xlii, p. 598 and 602, 1914. [Weese applies this name to *Pleonectria pinicola*.]

*Pleonectria calonectrioides* Wollenw. *Z. Parasitenk.*, iii, p. 493, 1931. (Teste Ehrlich in litt.)

#### DESCRIPTION

Under natural conditions, pycnidia are the first observable fructifications to develop on the host. These form on the surface of a stroma which develops in the cortex and ruptures the overlying periderm. It has a homogeneous pseudo-

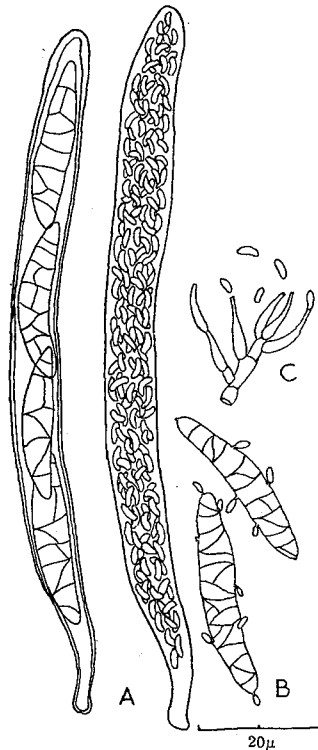


FIG. 4. *Thyronectria balsamea*. A, asci with ascospores and ascoconidia; B, ascoconidia forming ascoconidia; C, conidia and conidiophores from culture.

parenchymatic structure formed of elongate cells  $10-16 \times 6-9 \mu$ . The pycnidia are globose, deep red in colour with a dark-edged ostiole, and measure  $350-600 \mu$  in diameter. In section, the wall is  $25-30 \mu$  thick with 5-6 layers of cells. These tend to be compressed in the mature pycnidia but originally measured  $7-9 \times 5-7 \mu$ . The inner wall is especially convoluted in the basal region, and the whole

surface of the inner wall is covered with hyaline phialides  $10-16 \times 2 \mu$  at the base. Conidia are hyaline, allantoid,  $3-4 \times 1-1.5 \mu$ .

The perithecia generally develop round the pycnidia on the same stroma and are  $250-400 \mu$  in diameter, globose, with a rough outer wall covered with a furfureous coating, although this covering may be absent. They undergo pomiform to cupulate collapse on drying. The lateral wall is  $50-60 \mu$  thick and in the early stages of development has a homogeneous structure with the cells of the stroma; later it shows a gradation from the outer layers of thick-walled globose cells  $8-10 \times 6-8 \mu$  to the thinner-walled and more elongate cells of the inner layers where the cells measure  $9-12 \times 4-6 \mu$ . Elongate cells with thin walls line the perithecial cavity and these measure  $12-18 \times 2-3 \mu$ .

The asci are cylindrical to clavate with a rounded apex and measure  $70-130 \times 8-10 \mu$ , usually with four monostichous ascospores.

The ascospores are dictyospores with irregular septation and are hyaline, broadly fusiform,  $17-26 \times 4-6 \mu$ . Whilst still within the ascus they produce ascoconidia from short phialides or pores at each end of the spore. These ascoconidia are hyaline, allantoid,  $3-4 \times 1 \mu$ , and soon fill the whole lumen of the ascus, the ascospores finally disintegrating.

#### CULTURES

When isolated on to malt or potato dextrose agar the ascoconidia germinate to form hyphae which soon produce a sparse and somewhat floccose mycelium over the surface of the agar. From the hyphae short lateral pegs  $2-3 \mu$  long form in 5-6 days at  $22^\circ \text{C}$ . in the light; these small phialides form hyaline, allantoid microconidia,  $4-5 \times 1 \mu$ . The superficial hyphae soon give rise to dark stromatic pustules  $1-1.5 \text{ mm}$ . in diameter. In 5-6 weeks pycnidia begin to form as locules in the stroma and not as separate pycnidia. Each locule is lined by short-branched conidiophores which terminate in flask-shaped phialides  $6-20 \times 1-1.5 \mu$ . The only agar discoloration is a slight yellow tinge in the young cultures and a general darkening with age.

Most frequently recorded on dead bark of twigs and branches of *Abies balsamea*, but also on *Pinus sylvestris*, *P. strobus*, and *Psuga canadensis*.

#### SPECIMENS EXAMINED

*Nectria balsamea* folder Herb. R.B.G. Kew

*Co-type*; (ex Herb. Cooke) *Nectria balsamea* Cooke & Peck, on bark of dead balsam trees (*Abies balsamea*), North Elba, N.Y., July [1873]. Ex Herb. New York Bot. Gard., *Calonectria balsamea* (Cooke & Peck) Ellis & Everhart, on *Abies balsamea*, North Elba, N.Y., C. H. Peck.

*Thyronectria balsamea* folder Herb. I.M.I.

On *Abies balsamea*, Vermont, U.S.A., J.E., Aug. 34 (52268); Clear Lake, Dorset, Ontario, M. K. Nobles, Oct. 54 (DAOM 44894, I.M.I. 58091); loc. cit. Oct. 54 (DAOM 44897, I.M.I. 58092).

*Thyronectria lamyi* (Desm.) Seeler, *J. Arnold Arbor.*, xxi, p. 449, 1940.

*Sphaeria lamyi* Desm., Pl. Crypt. Fr., No. 389, 1836; *Ann. Sci. Nat.*, 2, VI, p. 246, 1836.

*Nectria lamyi* (Desm.) de Not., Sfer. Ital., 1, p. 13-14, 1863.

*Pleonectria lamyi* (Desm.) Sacc., Myc. Ven. Exs., vii, No. 688, 1876.

I have found no authentic British collection of this species; most British records refer to a misdetermination of *Nectria cinnabarina*. In the Herbarium of the Royal Botanic Gardens, Kew, there are seven collections from Cook's Herbarium.

Dr. Malcolm Wilson, in litt., states that these are parts of a collection of cryptogamic specimens given to the Edinburgh Botanical Society, in 1842, by Professor Rabenhorst and not British.

#### DESCRIPTION

Perithecia and pycnidia seated on small discrete stromata which develop in the cortex and rupture the overlying periderm. When the periderm is loose or absent the pycnidia and perithecia develop on a much-reduced stroma on the

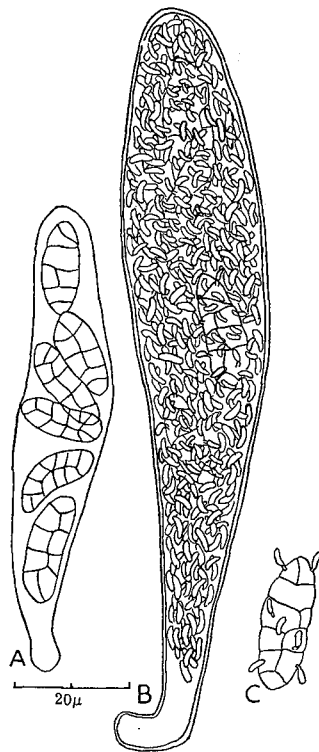


FIG. 5. *Thyronectria lamyi*. A, ascus with primary ascospores; B, ascus with ascoconidia; C, ascospore forming ascoconidia.

surface of the cortex. Only one to two pycnidia develop on each stroma, and they are similar to those of *Scoleconectria cucurbitula*, deep red with a large dark-edged ostiole and an irregular globose shape with a smooth wall; they measure 350-450  $\mu$  in diameter. The wall is 30-40  $\mu$  thick and formed of globose cells 5-7  $\mu$  in diameter. The cells of the outer 3-4 layers have thick reddish-brown walls whilst in the inner layers the cell walls are colourless. The inner wall of the

pycnidium is convoluted and the whole surface is covered with short-branched conidiophores terminating in narrow subulate phialides  $7-9\mu$  long and  $1-1.5\mu$  at the base. These phialides produce hyaline, allantoid conidia,  $3-4 \times 1\mu$  which fill the lumen of the pycnidium.

Perithecia develop round the pycnidium or on a distinct stroma. They are globose with a rough, often furfuraceous wall which is brownish red and darker round the ostiole; they often undergo a pomiform collapse when mature and measure  $300-350\mu$  in diameter. In section, the lateral wall is  $40-48\mu$  wide and is formed of globose to oblong cells  $8-10 \times 5-7\mu$ . The outer 3-6 layers have thicker brown walls and these merge into the rather thinner-walled cells of the inner layers. Lining the perithecial cavity are several layers of elongated thin-walled cells that become crushed in the mature perithecium.

The asci have a thin undifferentiated apex and are cylindrical to clavate when young with 6-8 subdistichous primary ascospores, they measure  $78-85 \times 12-14\mu$ . As the asci mature they become filled with ascoconidia and enlarge, becoming markedly clavate, and measure  $90-100 \times 22-24\mu$ .

The ascospores are hyaline, oval to oblong, with 5 transverse and 3-4 longitudinal septa, they measure  $15-29 \times 5.5-8\mu$  ( $20.2 \times 5.7\mu$ ). The ascospores are not discharged directly, each cell forms a small phialide from which ascoconidia are produced. These are hyaline, allantoid or cylindrical,  $3-4.5 \times 1-1.5\mu$ .

## SPECIMENS EXAMINED

*Pleonectria lamyi* folder Herb. R.B.G. Kew

Desm., Pl. Crypt. France, ser. 1, 18, No. 839 (1836), *Sphaeria lamyi* in ramis *Berberidis emortuis* (co-type issued with diagnosis). Rabenhorst, Fungi Europaei 752 (1865), *Nectria lamyi*. Rehm, Ascomyceten 39 (1870), *N. lamyi*. Sacc. Mycotheca Veneta 688 (1876), *Pleonectria lamyi* (Desm.) Sacc. (co-type material of *Pleonectria*).

*Thyronectria lamyi* folder Herb. I.M.I.

On *Berberidis vulgaris*, Hungary (Vindobon, Krypt. Exs. 822) *Pleonectria lamyi* (11401); North of Wilcox Lake, Ont., Canada, H. S. Jackson, May 32 (27031).

***Thyronectria berolinensis*** (Sacc.) Seaver, *Mycologia*, 1, p. 205, 1909.

*Pleonectria berolinensis* Saccardo, *Michelia*, 1, p. 123, 1878.

*Nectria berolinensis* (Sacc.) Cooke, *Grevillea*, xii, p. 107, 1884.

The identity of the fungus to which Tode applied the name *Sphaeria ribis* is uncertain. In published exsiccata it appears to have been applied to *Nectria cinnabarina* and *Pleonectria berolinensis* with equal frequency. The following table gives some indication of the use of the name by some of the mycologists who published exsiccata.

*Exsiccata issued as Nectria ribes with the writer's determination*

Plowright, Sphaer. Brit. iii. 11 (1878), *N. ribis* Fr. = *N. cinnabarina*

Vize, Microfungi Brit. ii. 153 (1879), *N. ribis* Fr. = *N. cinnabarina*

Sydow, Myc. Germ. viii. 389 (1905), *N. ribis* (Tode) Oud. = *N. cinnabarina*

Rehm, Ascom. xiii. 635b (1885), *N. ribis* Rab. = *N. cinnabarina*  
 Rabenh., Fung. Eur. iii. 247 (1860), *N. ribis* (Tode) Rab. = *T. berolinensis*  
 Jacz., Komarov & Tranz, Fung. Ross. ii. 81 (1895), *N. ribes* (Tode) Oud. =  
*T. berolinensis*  
 Griffiths, W. Amer. Fung. ii. 195 (1902), *N. ribis* (Tode) Rab. = *T. berolinensis*  
 Zahlbr., Mus. Palat. Vindob. ix. 820 (1903), *N. ribis* (Tode) Oud. = *T. berolinensis*

It can be seen from the table that *Nectria ribis* is a 'nomen confusum' and there is no justification for using this epithet in preference to *berolinensis* given to the species by Saccardo when he placed it in *Pleonectria*.

Fuchs (1913) reported four forms of spores in the life history of *Thyronectria berolinensis*, ascospores, ascoconidia (not in ascus), microconidia, resembling *Tubercularia vulgaris*, and a *Fusarium* macroconidial state. The latter was denied by Wollenweber (1913) and would in fact be quite alien to this group of *Nectrias*.

In many of the collections examined by me, having mature perithecia, the asci had disintegrated and the free ascospores were producing ascoconidia in the locule of the perithecium. Although I have not had fresh material of this species, sections of the conidial and perithecial stromata show the latter to develop round the former on the same stroma. The conidial stroma is a sporodochium and allied to *Nectria aquifolii* and *N. coryli*.

#### DESCRIPTION

A conidial stroma in the form of sporodochium precedes the perithecial formation. The sporodochial stromata are 0.6–1 mm. in diameter and are formed of host and fungal tissues in the lower layers. The upper 80–100  $\mu$  is almost all fungal tissue formed of a pseudoparenchyma of homogeneous thin-walled cells 8–12  $\mu$  in diameter. The surface is covered with a palisade of hyphae which are 90–120  $\mu$  long and formed of upright, occasionally branched, filaments 2–3  $\mu$  wide which terminate in a swollen, rough-walled tip. The individual cells are 16–20  $\mu$  long and often form small lateral phialides near the tips. These phialides are 4–7  $\mu$  long and 1.5–2  $\mu$  near the base, narrowing slightly towards the apex where the lateral wall is thickened to form a collar. The conidia produced from these phialides are hyaline, cylindrical, aseptate, and measure 6–9  $\times$  2–2.5  $\mu$ ; they cover the sporodochium with a cream-coloured layer.

Perithecia may develop round the conidial stroma, or on a separate stroma. The perithecia are globose to ovoid but often misshapen by mutual compression. The outer wall is rough, often fissured, red to deep brownish red in colour and slightly darker round the ostiole; no apical papilla is present. They tend to undergo a pomiform collapse when dry, and measure 300–375  $\mu$  in diameter. In section the wall is 40–50  $\mu$  wide and formed of two regions. Actually, the outer, which forms the greater part of the wall, has an outer region of 3–4 layers of globose, brown, and apparently dead cells which measure 4–6  $\mu$  in diameter. These merge into the layers of oval to oblong cells which measure 6–9  $\times$  3–5  $\mu$ . The fissures often visible on the surface of the wall extend through the brown cells only. The cells of the inner region line the perithecial cavity, they are elongate, hyaline, with very thin walls.

The asci are cylindrical with a rounded thickened apex bearing a pore, they



have eight monostichous and later obliquely monostichous ascospores and measure  $90-110 \times 10-12 \mu$ . No evidence of ascoconidial formation in the ascus was found.

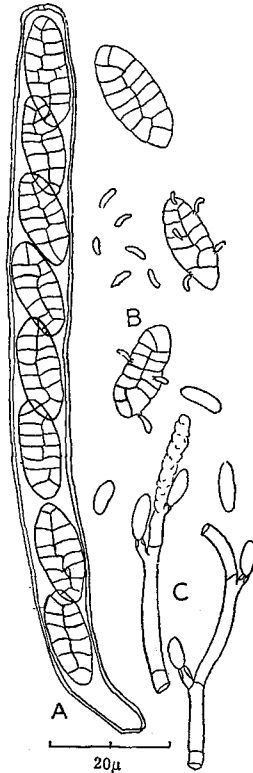


FIG. 6. *Thyronectria berolinensis*. A, ascus with ascospores; B, free ascospores forming conidia; C, conidia and conidiophores from host.

The ascospores are smooth, hyaline, cylindrical, with bluntly rounded ends, 5-7 transverse septa, and 1-2 incomplete longitudinal septa. They become straw-coloured when mature and measure  $18-20 \times 6-8 \mu$ . When the ascospores are released from the ascus they begin to form ascoconidia from small phialides or pores in the wall. These conidia are allantoid to oval, hyaline, aseptate,  $2.5-3.5 \times 1 \mu$ .

#### SPECIMENS EXAMINED

*Pleonectria berolinensis* folder Herb. R.B.G. Kew

Ellis, N. Amer. Fung. v. 470 (1880); Rabenh.-Winter, Fung. Eur. xxxvii. 3650 (1890); Zahlbr., Krypt. Exs. ix (Mus. Palat. Vindob.) 820 (1903); Sydow, Myc. Germ. xvii. 896 (1910); *ibid.* xxii. 1593 (1921); Petrak, Fungi Polon. Exs. xx. 500 (1920); Fungi Alban. et Bosn, Exs. vii. 157 (1921); Myc. Carpat. xi. 257 (after 1921); Farlow Herb., Harvard Univ., Reliq. Farl. 1, 74 (1922).

*Nectria ribis* folder Herb. R.B.G. Kew

Rehm, Ascomyceten 634 (1882), *Pleonectria ribis* = *T. berolinensis*.

*Nectria berolinensis* folder Herb. B.M. Nat. Hist.

Sydow, Myc. March. xxxii. 3139 (1891); Ellis & Everh., Fungi Columb. 1, 26 (1893); *ibid.* vii. 619 (1895); Vestergren, Micromyc. Rar. Sel. xxxvii. 925 (1905); Wilson & Seaver, Ascom. and Lower Fungi, iii. 67 (1909).

*Nectria ribis* folder Herb. B.M. Nat. Hist.

Jaczewski, Komarov & Tranzschel, Fungi Ross. Exs. 11, 81 (1895); Griffiths, W. Amer. Fungi, 11, 195 (1902).

*Thyronectria berolinensis* folder Herb. I.M.I.

On *Ribes*, Kulm, U.S.A., F. Brenckle (Fung. Dakotenses 125), July 09 (18460); Nyland Grove, Lamoure County, U.S.A., F. Brenckle (Fung. Dakotenses 239), May 13 (18461); Winnipeg, Man., Canada, G. R. Bisby, May 22 (31211); Tamsel, Germany, P. Vogel (Flora der Mark.), Nov. 26 (31210); Sternberg, Austria, J. Piskor (Petraik, Myc. gen. 1861), Nov. 30 (33338); Brant Co., Ont., Canada, R. F. Cain, Mar. 32 (27030); Vidsmuifr., Latvia, K. Starcs, Jan. 34 (31212); Winnipeg, Man., G. R. Bisby & B. Brown, June 35 (26917).

#### THE CINNABARINA GROUP

This group is represented in Britain by the following species: *Nectria cinnabarina*, *N. aurantiaca*, and *N. ralfsii*.

The perithecia form on a well-developed stroma either alone or grouped round the conidial fructification, they are rough-walled to warted and in section the wall is seen to be formed of globose cells loosely attached in the outer layers. These cells form the warts or give the powdery appearance to the wall.

Asci are clavate with an undifferentiated apex and obliquely monostichous to distichous ascospores which may be variable in shape and size within a single ascus.

The conidial stroma is primarily sporodochial but in *Nectria aurantiaca* it is a synnema.

The conidia are typically hyaline, oval to cylindrical and aseptate. *N. ralfsii* is atypical in having dark, lemon-shaped conidia.

Cultures show little agar discoloration, sparse white aerial mycelium, and pustules of hyphae forming scattered sporodochia or synnemata.

In Tulasne's (1865) diagnosis of the genus *Sphaerostilbe* the only distinction that is made between it and the genus *Nectria* is the method of conidial formation. Apart from the close similarity between the perithecial structure and appearance of *Nectria cinnabarina* and *N. aurantiaca* there is a structural similarity of the conidiophores and conidia. In fact the only distinction is the stalked *Stilbum*-like conidiophores of the latter. That this character is not of generic value is evident from an examination of the early conidial fructifications of *Sphaerostilbe aurantiaca*, these are without a stalk and should therefore be assigned to the genus *Tubercularia* and not *Stilbum* or *Stilbella*.

The tendency to form a short synnema is also found in *Nectria cinnabarina* and the variety *N. cinnabarina* var. *dendroidea* Wollenweber (1926) was based on this character.

*Nectria ralfsii* is unusual amongst British nectrias in having dark lemon-shaped conidia, but it is clearly allied to the other two species in its method of conidial formation and in the structure of the perithecium.

## KEY TO SPECIES

Perithecia yellow, following or associated with a <i>Myrothecium</i> conidial state	<i>N. ralfsii</i>
Perithecia red, following or associated with a 'Tubercularia or Stilbum' conidial state	
Ascospores $16.3 \times 5.9 \mu$	<i>N. cinnabarina</i>
Ascospores $21.5 \times 7.5 \mu$	<i>N. aurantiaca</i>

***Nectria cinnabarina*** (Tode ex Fr.) Fries, Summa Veg. Scand., ii, p. 388, 1849.

*Sphaeria cinnabarina* Tode, Fung. Meckl., ii, pp. 9-10, 1791. Ex Fries, Syst.

Mycol., ii, p. 412, 1823.

*Cucurbitaria cinnabarina* (Tode ex Fr.) Grev., Scot. Crypt. Fl., iii, p. 135, 1825.

*Nectria russellii* Berk. & Curt. apud Berk., *Grevillea*, iv, p. 45, 1875.

*Nectria offuscata* Berk. & Curt. apud Berk., *Grevillea*, iv, p. 45, 1875.

*Nectria nigrescens* Cooke, *Grevillea*, vii, p. 50, 1878.

*Nectria fusco-purpurea* Wakef., *Kew Bull.*, p. 232, 1918.

*Sphaeria decolorans* Pers., Syn. Meth. Fung., p. 49, 1801. Fries, Syst. Mycol., ii, p. 412, 1823.

*Tubercularia vulgaris* Tode ex Fries, Syst. Mycol., iii, p. 464, 1832.

Few of the early microfungi are more soundly established, by the original figure and description, than *Nectria cinnabarina*.

Tode (1791) described it as a simple *Sphaeria* with oval, granular, and apically depressed perithecia surrounding *Tremella purpurea* L., our *Tubercularia vulgaris*. This description was supported by four figures.

Fries (1823) took up the name *Sphaeria cinnabarina* with the following diagnosis:

Group. Caespitosae: *Sphaeria cinnabarina*, caespitosa, peritheciis globosis corrugatis cinnabarinis decolorantibus, ostiolo pillulaeformi.

H. A. Jorgensen (1952) published a monograph on *Nectria cinnabarina* in which both the taxonomic and pathogenic aspects are dealt with exhaustively; evidence is given supporting the view that this species is a facultative parasite and saprophyte. He found no cultural or morphological variations between his different isolates of the fungus from different hosts except those from *Ribes*. The fungus resembling *N. cinnabarina* on *Ribes* has been called *N. ribis*. Jorgensen considers it as a variety of *N. cinnabarina* because of the somewhat larger average size of the ascospores and conidia and its higher growth-intensity in culture. In any case *N. ribis* (Tode ex Fr.) Rab. is a 'nomen confusum' (see p. 24).

My isolations from different hosts support Jorgensen's finding. These isolations were chosen from the abundant material available because they showed some variation from normal in their appearance. They formed identical cultures and no constant morphological difference was observed that would justify their separation as varieties. Unfortunately, I have had no fresh material from *Ribes*, but collections on this host examined by me that have been disposed in herbaria as *Nectria ribis* and *N. cinnabarina* on *Ribes* show a close relationship to each other and to *N. cinnabarina* on other hosts.

*Nectria cinnabarina* has a wide host range, and the superficial appearance of the perithecia is often related to the conditions under which they developed.

## DESCRIPTION

Usually the first indication of the presence of *Nectria cinnabarina* is the protrusion of scattered discrete stromata through the periderm of the host. These are 350–500  $\mu$  in diameter and orange to orange-red in colour. Phialides arise just below the surface of the stroma and the overlying tissue is split and folds

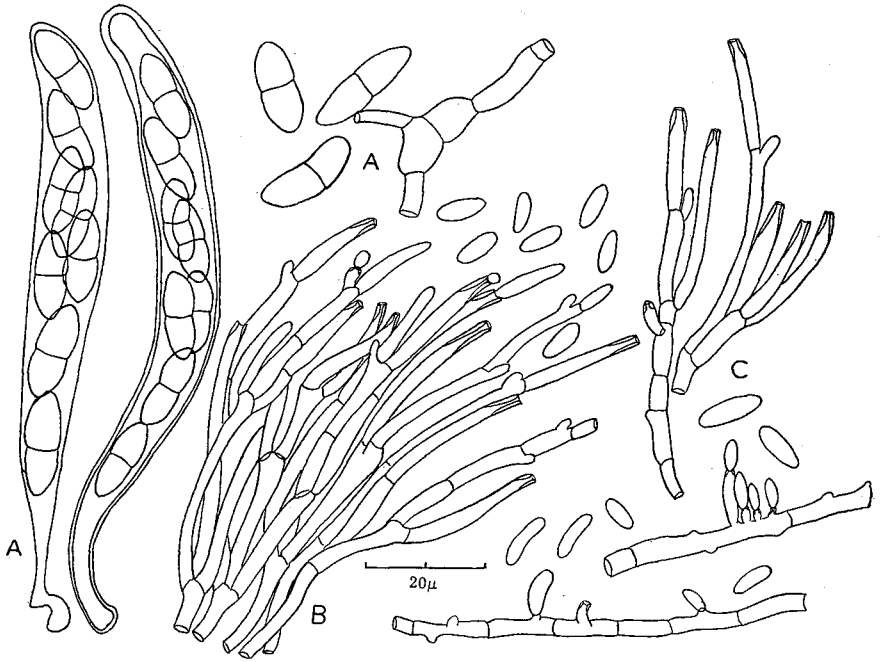


FIG. 7. *Nectria cinnabarina*. A, mature asci and ascospores, one ascospore germinating; B, conidia and conidiophores from host; C, conidia and conidiophores from culture.

back. This tissue probably acts as a protective covering as the stroma forces its way through the periderm. The phialides are formed laterally or as terminations to short-branched hyphae which arise from the pseudoparenchymatic stroma. They are subulate 20–30  $\mu$  long and 2–3.5  $\mu$  at the base and become somewhat narrower towards the apex where the lateral wall is thickened to form a collar. Masses of cylindrical to oval conidia 5–7  $\times$  2–3  $\mu$  are formed from the phialides and these cover the top of the sporodochia with a cream, and later coral-coloured, layer of conidia.

Perithecia frequently form round the edge of the conidial stroma or may develop on a separate stroma in groups of 1–15. They are globose with a pomiform collapse and a rough crustaceous outer wall, red to brazil red in colour, and at times appear to be dusted with a white powder; this appearance is caused by the disintegration and separation of the dead cells of the outer wall. In section the wall is 50–60  $\mu$  thick and formed of two regions. The outer region shows considerable variation in the size of cells, these are globose 10–16  $\mu$  in diameter or oblong 12–24  $\times$  8–10  $\mu$  in the outer layers, but the inner layers are a mixture of these large cells and smaller globose cells 4–8  $\mu$  in diameter. The

inner region is 10–12  $\mu$  wide and formed of very thin-walled elongate cells which are crushed in the mature perithecium.

The asci are cylindrical with a thin rounded apex; later they may become more clavate as the ascospores become subdistichous. They measure 60–90  $\times$  9–14  $\mu$ .

The ascospores often show a variation in size within a single ascus, they are cylindrical to ellipsoid, hyaline, and slightly constricted at the central septum. They measure 12–20  $\times$  4.5–6.5 (16.3  $\times$  5.9)  $\mu$ .

#### CULTURES

Ascospores germinate readily producing one or more hyphae from each cell, conidia may develop from lateral pores, or poorly developed phialides, on these hyphae in 24 hours. These conidia are hyaline, cylindrical 4–7  $\times$  2–2.5  $\mu$ . The surface of the agar is covered with a white cottony mycelium in about 4 weeks and aggregations of hyphae form stromatic initials. No discoloration of the agar occurred except darkening as the agar dried out. These white stromatic pustules form sporodochia covered with phialides as on the host but the structure is loose, white, and more cottony in texture. The surface becomes covered with hyaline, cylindrical to fusoid conidia that measure 5–7  $\times$  2–3  $\mu$ .

#### SPECIMENS EXAMINED

*Nectria cinnabarina* folder Herb. R.B.G. Kew

Fries, Scler. Suec. 184 (1821), *Sphaeria decolorans*. Fuckel, Fung. Rhen. 978 (1864), *Nectria cinnabarina* Fr., 2657 *N. cinnabarina* Tul. Rabenhorst, Fung. Europaei 324 (1861), *N. cinnabarina* (Tode) Fr. Rehm, Ascomyceten 184 (1873), *N. cinnabarina* (Fr.) Tul. f. *obscura*. Miki, 282 (1875) *N. cinnabarina* (Fr.) Tul. Roumeguère, Fung. gallici 982 (1880) and 1466 (1881) *N. cinnabarina* var. *minor* and *N. cinnabarina*, 1173 *N. tiliae* Karst (*N. cinnabarina* f. *tiliae*). Sydow, Mycotheca Mar. 888 (1884), 909 (1885), and 1150 (1886) *N. cinnabarina*, Mycotheca germanica 80 (1903), *N. cinnabarina* (Tode) Fr. Baxter, Stirpes Crypt. Oxon, 26 (1825), *Cucurbitaria cinnabarina* Grev. U.S. Dept. agric., Path. & Mycol. 1549 *N. cinnabarina* (Tode) Fr. on *Ribes*.

*Nectria fusco-purpurea* folder Herb. R.B.G. Kew

*Nectria fusco-purpurea* Wakef., on plum.

*Nectria nigrescens* folder Herb. R.B.G. Kew

*Nectria nigrescens* on *Gleditschia*, Ravenel 2380.

*Nectria offuscata* folder Herb. R.B.G. Kew

*Sph. offuscata* B. & C., 2865 Car. Inf. (Herb. Berk.).

*Nectria russellii* folder Herb. R.B.G. Kew

*Nectria russellii* Berk. & Curt. 5447.

*Nectria aurantiaca* (Tul.) Jaczewski, Opredlitel gribov, Tom. 1 (Key to Fungi, 1 Perfect fungi), p. 215, 1913.

*Sphaerostilbe aurantiaca* Tul., Sel. Fung. Carp., 1, p. 131, 1861 (Groves' Translation).

*Nectria aurantiaca* (Tul.) Wollenw., *Angew. Bot.*, viii, p. 186, 1926.

*Stilbum aurantiacum* Babington ('in *Abstr. of Linn. Soc. Trans.*, 1839') ex Berk. & Br., *Ann. Mag. nat. Hist.*, ser. 1, vi, p. 432, 1841.

*Stilbella aurantiaca* (Babington) Lindau in Rabenh., Krypt. Fl., 1, ix, p. 298, 1908.

*Ditiola tubercularioides* Libert in Herb., No. 470 (Kew, ex Herb. Hort. Bot. Bruxelles; et Roum. Exs. 1788).

*Ciliciopodium tubercularioides* (Libert) Sacc., Fung. Ital. del. tab. 755, 1881.

All the collections of this species examined by me have been on *Ulmus*. The justification for maintaining it in a distinct genus based purely on its conidial state has been rejected in the introduction to this group.

#### DESCRIPTION

Conidia form before, and often distinct from, the perithecia, although the latter typically form round the base of the conidial fructification. Although this



FIG. 8. *Nectria aurantiaca*. A, mature ascus and free ascospores; B, conidia and conidiophores from host; C, conidia and conidiophores from culture.

is usually in the form of a synnema the first-formed conidia are on a sporodochium. This arises in the cortex and ruptures the overlying periderm, and measures  $300-500\ \mu$  in diameter. Synnemata are formed in a similar position but the component hyphae elongate to form the stalk which bears the characteristic cream-coloured head. The synnemata are erect, cylindrical or flattened, taper from the base to below the rounded apex, and measure 1-2 mm. high and  $75-125\ \mu$  wide at the base. They are brazil red at the base but lighter above with a cream-coloured head. The stalk is formed of parallel and frequently anastomosed hyphae with cells  $20-24 \times 2-3\ \mu$ . The hyphae are shortly branched at the apex and each branch terminates in a subulate phialide  $25-35\ \mu$  long and  $2-3\ \mu$  at the base. Conidia produced from these phialides are hyaline, cylindrical, aseptate with a thick wall, and measure  $16 \times 6\ \mu$  ( $12-19 \times 6-7\ \mu$ ). They accumulate on the synnema to form a cream-coloured head.

The perithecia occur in small groups on an erumpent stroma or, as stated, round the base of the conidial stroma. They are brick red, globose with a rough warty outer wall. The ostiolar region is conical, smoother, and darker than the rest of the wall. In section the lateral wall is  $60-70\ \mu$  wide; it may be divided into two regions although these are not very distinct. The outer is formed of large globose cells  $10-12$  or oval  $8-12\ \mu$ , interspersed with these, especially in the inner layers of this region, are smaller globose cells  $4-8\ \mu$  in diameter. The inner region  $20\ \mu$  wide has elongated cells  $10-16 \times 2-3\ \mu$ , the walls of these cells become gradually thinner towards the perithecial cavity and those forming the lining to the cavity become crushed as the perithecium matures.

The asci are  $95-125 \times 16-22\ \mu$ , clavate with a thin rounded apex and with eight obliquely monostichous to distichous ascospores.

The ascospores are elliptical, some inequilateral, smooth, becoming pale brown with a slight constriction at the central septum; they measure  $21.5 \times 7.5$  ( $17-26 \times 7-9$ )  $\mu$ .

#### CULTURES

Ascospores germinate to form a hyphal primordium at each end of the spore which gives rise to a sparse mycelium. Conidia are formed from short lateral phialides along the hyphae in 3-4 days in light at  $22^\circ\text{C}$ . on both potato dextrose and malt agar.

In 7-10 days pustules of branched hyphae form sporodochia that are covered with phialides  $20-24\ \mu$  long and  $2-2.5\ \mu$  at the base. Conidia formed from these are hyaline, cylindrical, aseptate, and measure  $12-19 \times 4.5-6\ \mu$ , these are rather narrower than those found on the host and have thinner cell walls. No discoloration occurs in the media. In older cultures the sporodochial primordia grow upwards and form synnema; the stalks of these remain hyaline and the hyphae are not so compressed as in the synnema found on the host. They are 1-1.5 mm. long and  $100-150\ \mu$  wide and terminate in a globose head which, as on the host, becomes covered with cream-coloured conidia.

Mature cultures are covered with sparse aerial mycelium with synnemata dispersed over the surface, the agar becomes darker as it dries out but there is no pronounced discoloration. Conidia formed in culture germinate readily.

## SPECIMENS EXAMINED

*Sphaerostilbe aurantiaca* folder Herb. R.B.G. Kew

On *Ulmus*, Elmhurst, Berk. 28, xii, 1852, ex Herb. Berk.

*Ciliciopodium tubercularioides* folder Herb. R.B.G. Kew

Ex Herb. Jard. Bot. Bruxelles *Ditiola tubercularioides* sur *Ulmus*, Lib. in Herb. (& pencilled) *Ciliciopodium tubercularioides* Coll. Libert No. suppl. 470. Roumeg. Fung. gall. Exs. 1788 (1881), *C. tubercularioides* (Lib.) Sacc.

*Nectria aurantiaca* folder Herb. I.M.I.

On *Ulmus*, nr. Bristol, E.W.M., Oct. 29 (50376), this collection was cited by Wollenw. Fus, Auto. del. 789; Blockley, Glos., C. G. C. Chesters, Nov. 34 (22785); Brailes, S. Warwicks., E.A.E., Nov. 55 and Aug. 56 (62101a and 63581).

*Nectria ralfsii* Berk. & Br., *Ann. Mag. nat. Hist.*, ser. 2, xiii, p. 467, 1854.

*Nectria daldiniana* de Not., *Sfer. Ital.*, I, p. 12, 1863.

*Calonectria verruculosa* Niessl apud Thümen., *Rev. Sci. Litt.* Coimbra, xxvii, 1879; (in separate pp. 31-32, No. 288).

*Nectria verruculosa* (Niessl.) Penzig, *Michelia*, ii, p. 420, 1882.

The writer has only obtained conidial material of this species and these failed to germinate. The species has, however, been grown by Mr. E. W. Mason and these cultures and the material from which they were obtained are deposited in Herb. I.M.I. under No. 1530. A note written by Mr. Mason and published by Rilstone (1941) is reproduced in part here.

Miss Wakefield collected the *Nectria* on the Totnes Foray of the British Mycological Society from the middle of a pile of cut brush-wood, and I isolated the ascospores and got the conidia in culture. They were abundantly present and in association with the *Nectria* perithecia. I had a browse round herbarium specimens with the following results; the conidia are present on authentic material of *N. ralfsii* Berk. & Br.; also on authentic material of its synonyms *Nectria daldiniana* de Not. (Italy) and *Calonectria verruculosa* Niessl (Portugal). Niessl saw these conidia, as he described the perithecia; 'ut videtur parasitans in pyreniis stylosporiferis Anthostomellae.' They also received a name, partly their own, in Portugal—*Sphaeropsis henriquisii* Thümen—for I found the perithecia of *N. ralfsii* on authentic material of that so-called *Sphaeropsis*. Thümen was quite mistaken in thinking that the conidia are borne in the pycnidia he described; they are not, and the fungus cannot possibly be classified as any sort of *Sphaeropsis*. I recommend holding the fungus as conidial *Nectria ralfsii*; it is a Mediterranean species and should be not uncommon in our south-western peninsula. It is not host-limited and can probably be found by turning over piles of sticks.

There is no record of the distribution of this species in Britain having been extended since this date and my collection was from the Bristol area.

Weese (1918) in his description of this species claimed that the ascospore measurements given by Saccardo, *Syll. Fung.* ii, p. 492 and by Winter, *Rhab. Krypt. Fl.* I, ii, p. 119, 1887 for *N. daldiniana* are incorrect. He claims that both Fuckel and Bref. & Stav. dealt not with *N. daldiniana* but with some form of *N. ochroleuca*.



## DESCRIPTION

The stroma may be discrete or elongated along the fissures of the periderm, it arises in the cortex and ruptures the overlying periderm. Basally it is formed of loosely anastomosed hyphae, but the erumpent part is pseudoparenchyma and it is from this that the conidiophores and perithecia develop.

Conidiophores form a sporodochium on the surface of the young stroma and this may be referred to the imperfect genus *Myrothecium*. The stalk of the conidiophore is 5-6  $\mu$  wide and bears apically 3-4 cells 18-22  $\times$  6  $\mu$ . Each of

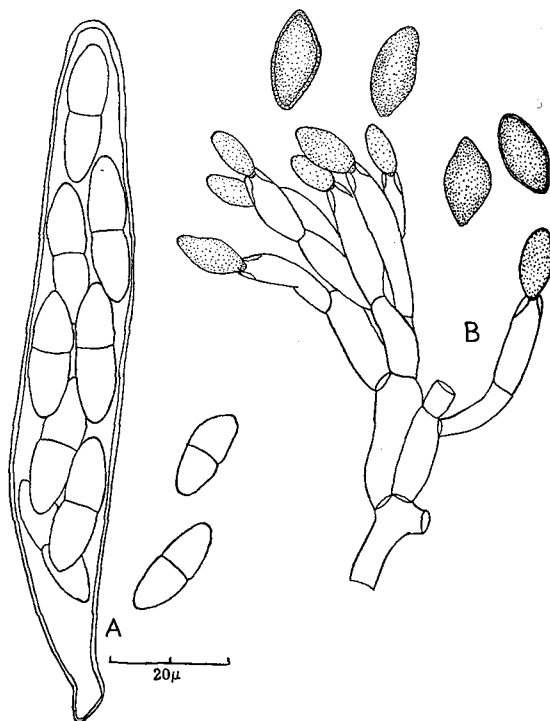


FIG. 9. *Nectria ralfsii*. A, ascus and ascospores; B, conidia and conidiophores from host.

these cells bears 2-4 apical cells and these terminate in 1-2 phialides, thus the conidiophores have a compact penicillate branching. The phialides are doliform 13-25  $\times$  4-5  $\mu$ . Conidia produced from these are lemon-shaped, aseptate, hyaline at first but as they develop a thick wall they become greenish in colour; they measure 11-17  $\times$  6.5-8  $\mu$ .

The perithecia develop round the edge of the conidial stroma. They are yellow to orange, flattened globose, and show a pomiform to almost cupulate collapse when mature, the surface appears granular or warted, and in diameter they measure 320-400  $\mu$ . In section the lateral wall is 75-85  $\mu$  wide and formed of two regions. The outer region which occupies the greater part of the wall is 60-70  $\mu$  wide; the outer 6-8 layers of this region are formed of loosely attached globose cells 8-11  $\mu$  in diameter; below are 4-5 layers of oval cells 8-12  $\times$  4-6  $\mu$ .

The inner region is 15-20  $\mu$  wide and formed of elongated thin-walled cells that are crushed in mature perithecia.

The asci are clavate, shortly stipitate with a rounded undifferentiated apex and eight usually distichous ascospores, they measure  $75-96 \times 12-16 \mu$ .

The ascospores are elongated elliptical and slightly constricted at the central septum; they are hyaline, smooth-walled, and somewhat variable in size in the ascus; they measure  $18-23 \times 6-8 \mu$ .

#### CULTURES

Cultures on 2 per cent. maize meal agar have sparse, white aerial mycelium and little discoloration of the agar, loose sporodochia are scattered over the surface and these produce masses of dark green conidia which are more irregular in shape than those found on the host and without such a marked thickening of the wall; they measure  $10-14 \times 7-8 \mu$ .

#### SPECIMENS EXAMINED

*Nectria ralfsii* folder Herb. R.B.G. Kew

*Nectria ralfsii* B. & Br. (*S. salmonicolor* Berk.) *Ulex*, Penzance; *Nectria ralfsii* on *Fagus* (all three parts of this are on *Acer* and this is the type collection). *N. peziza*, Cornwall, J. Ralfs (Broome in litt.), Jan. 5th 1852; Rabenhorst, *Fungi europaei* 2041 (1880), *Nectria ralfsii*.

*Nectria verruculosa* folder Herb. R.B.G. Kew

*Calonectria verruculosa* Niessl on *Citri limoni*, J. Henriques, 1878; *Calonectria verruculosa* Niessl on *Citrus*, Portugal, Ex Herb. Cath. de Thümen, *Mycotheca universalis* 1550 (1880), *Calonectria verruculosa* Niessl; Roumeguère, *Fungi Gall. exs* 4760 (1889), *Nectria verruculosa* (Niessl) Penzig.

*Nectria ralfsii* folder Herb. I.M.I.

On *Acer*, Berry Pomeroy, Devon, E. M. Wakefield, Sept. 35 (1530); Cleeve Coombe, Bristol, A. H. S. Brown, Sept. 55 (61054d). On *Carmichaelia*, Little Berries Is., Auckland, N.Z., J. M. Dingley, Dec. 47 (50401). On *Coprosma*, Moumaukai Valley, Auckland, N.Z., J. M. Dingley, 54 (70018). On *Edwardsia*, Pika, Auckland, N.Z., J. M. Dingley, Jan. 47 (50410); Whangarei, Auckland, N.Z., J. M. Dingley, Oct. 47 (49992). On *Ulmus*, Perranzabuloe, Cornwall, F. Rilstone, Jan. 49 (33897). On *Pyrus*, Perranzabuloe, Cornwall, F. Rilstone, Dec. 38 (33897) (1533). On *Wintera*, Otago, Lower Holyford, N.Z., J. M. Dingley, Mar. 51 (49989).

#### THE OCHROLEUCA GROUP

This group is represented in Britain by *Nectria pallidula* and provisionally by *N. solani* and *N. keithii*.

*Nectria ochroleuca* was described by Schweinitz (1832) and numbered 144 in his collection. Unfortunately, Schweinitz often included several collections of what he took to be the same species under one number and therefore the 'Type' material cannot be ascertained. Part of the material under this number in Schweinitz's herbarium was sent to Berkeley by Curtis after Schweinitz's death. Examination of this material now in Herb. R.B.G. Kew shows it to be distinct from any British species so far collected.

This group forms a large and important section of the tropical *Nectria* spp. The British species represent the mere fringe of the group which has not been sufficiently defined to form a homogeneous unit. The species are typified by their smooth to warted, yellow perithecia seated on a stroma. This is generally pseudoparenchymatous but is partially byssoid in two of the British species. The conidial states which belong to the genus *Gliocladium* can only be distinguished from each other by critical examination.

Two of the three British collections cited as *Nectria ochroleuca* and included by Petch (1938) were found to be *N. pallidula* and the other was *N. citrino-aurantia*. Petch cited them as confirmed by Ehrlich, however, Ehrlich (in litt. Herb. I.M.I.) was appalled by the confusion existing in this group and merely hoped to draw attention to it. He did not consider himself competent to determine the species. I have seen no British collections of *N. ochroleuca*.

Petch also in 1938 cited *Nectria keithii* as a synonym of *N. subquaternata*. This latter species was described by Berkeley and Broome from a collection made in Ceylon by Thwaites (No. 173). It has since proved to be one of the most common tropical *Nectrias* but it is quite distinct from *N. keithii*.

*Nectria keithii* and *N. solani* are rare British species, and are imperfectly known from the few collections obtained. The perithecial and conidial states of *N. solani* were described by Reinke and Berthold. No further record has been found of the ascospores having been grown.

## KEY TO SPECIES

- |  |                     |
|--|---------------------|
| 1. Perithecia aggregated on a pseudoparenchymatous stroma, ascospores<br>10-14 × 3.5-5 μ | <i>N. pallidula</i> |
| 1. Perithecia seated on a byssus or scattered  |                     |
| a. Ascospores 8-12 × 3.5-5 μ: on <i>Brassica</i> stems                                   | <i>N. keithii</i>   |
| b. Ascospores 10-14 × 3.5-5 μ: on potato tubers  | <i>N. solani</i>    |

*Nectria pallidula* Cooke, *Grevillea*, xvii, p. 3, 1888.

Most of the British records of *Nectria ochroleuca* have been found to be *N. pallidula*. The conidial state is similar to that recorded for *Nectriopsis aureonitens* but this has denser penicillate heads with smaller phialides and conidia than *Nectria pallidula*.

## DESCRIPTION

The perithecia develop in succession on a weakly erumpent stroma that increases in size with age. This stroma, which develops in the cortex and ruptures the overlying periderm, is formed at first as a fascicle of hyphae but these fuse later to form a loose pseudoparenchymatous stroma. Both the stroma and the perithecia are yellow but may become straw-coloured with age. The perithecia are globose 250-300 (250-375) μ in diameter with a finely roughened wall and a small, light brown, ostiolar papilla. The lateral wall is 35-50 μ thick and consists of four regions. The outer, which is continuous with the wall of the stroma, is 20-25 μ thick and formed of globose cells 7-9 μ in diameter or elongated cells 8-14 × 5-7 μ. Below is a region 8-12 μ wide formed of a reticulum of hyphae 2-3 μ wide which may disintegrate in parts as the perithecium matures. The third region is 6-9 μ wide and formed of densely compacted elongate cells;

apically these cells form parallel hyphae which give rise to the ostiolar disc. The fourth and inner region is formed of 3-4 layers of very thin-walled cells which become compressed as the asci mature.



FIG. 10. *Nectria pallidula*. A, asci and ascospores; B, conidia and conidiophores of *Gliocladium penicillioides* from C.B.S.; C, conidia and conidiophores of *Nectria pallidula* from culture.

The asci are clavate with a short stalk and a rounded apex bearing a central ring, they measure  $55-80 \times 7-12 \mu$ . In the young asci the ascospores are obliquely subdistichous but when mature the ascospores tend to aggregate in the upper part of the ascus.

The ascospores are broadly fusoid and slightly constricted at the single central septum; when mature they are slightly roughened, become light brown, and measure  $10-14 \times 3.5-5 \mu$ .

#### CULTURES

The ascospores swell before germination and then produce a hyphal primordium from each cell of the spore. Growth at  $21^{\circ}$  C. was dense but slow, after 21 days it extended 3 cm. down the tube and by this time extensive conidial production was occurring. The aerial mycelium was white, but the culture from below was salmon pink on maize meal agar and pinkish brown on malt agar. Apart from a darkening with age no further agar discoloration occurred, the aerial mycelium remained floccose, and abundant conidiophores were formed over the surface. No perithecia developed either in agar cultures or in cultures on sterilized elm twigs.

The first conidia are formed on relatively complex conidiophores. These begin to develop after 6-8 days as an upright stipe from the superficial hyphae which are  $2 \mu$  wide. The stipe is  $100-180 \mu$  long and branches once or twice at the apex. The secondary branches, which may be termed metulae, bear 2-4 phialides at the apex. These are hyaline obclavate,  $14-23 \mu$  long and  $2.5-3 \mu$  at the base, they narrow towards the apex which terminates in a collar formed by a thickening of the lateral wall. Conidia formed from these are hyaline, oval, often somewhat irregular, and measure  $4-7 \times 2-3 \mu$ .

Thicker hyphae  $2.5-4.5 \mu$  wide develop in the cultures after about 14 days, these also produce conidiophores which are similar to those described but have a thicker stipe and a more densely branched and compacted head. The conidia produced are indistinguishable from those of the earlier conidiophores.

#### SPECIMENS EXAMINED

*Nectria pallidula* folder Herb. R.B.G. Kew

*Nectria pallidula* Cke, Carlisle, Sept. 1885, Dr. Carlyle (on *Fagus*, scripsit Cooke). Type collection. On *Fagus*, Carlisle, Dr. Carlyle 1888.

*Nectria ochroleuca* folder Herb. R.B.G. Kew

On Wych elm (*Ulmus glabra*), Forden, Vize, No. 2. On indet. wood, Coed Coch, Oct. 1880 (Cooke as *N. ralfsii*).

*Nectria pallidula* folder Herb. B.M. Nat. Hist.

On *Fagus*, Carlisle, Dr. Carlyle (ex Herb. Masee, part of Type coll.). On broom, North Wootton, Oct. 34 and Mar. 35.

*Nectria ochroleuca* folder Herb. B.M. Nat. Hist.

On roots of horse-chestnut (*Aesculus hippocastanum*), Birmingham, Sept. 1886 as *Nectria ochroleuca*.

*Nectria pallidula* folder Herb. I.M.I.

On *Acer*, Cleeve Coombe, Bristol, A. H. S. Brown, Sept. 55 (61054a) and J.W., Sept. 55 (71731). On *Robinia*, Moulin Huet, Guernsey, M. B. & J. P. Ellis, Sept. 48 (33709). On *Solanum*, Wheatfen Broad, Norfolk, E.A.E., Aug. 46 (6358).

*Nectria keithii* Berk. & Br., *Ann. Mag. nat. Hist.*, ser. 4, xvii, p. 144, 1876.

*Nectria keithii* was included by Petch (1938) as a synonym of *N. subquaternata*. This species is a common tropical *Nectria* but I have found no British collections. The processes surrounding the ostiole of *N. keithii* were apparently mistaken for the warts found on the perithecia of *N. subquaternata*. *N. keithii* has been found twice in Britain since the collection described by Berkeley and Broome.

The very characteristic perithecia are closely associated with a *Gliocladium* state which is markedly different from the *Gliocladium* state of *Nectria subquaternata*. *N. keithii* also differs from this species in the smaller, thinner-walled cells in the outer layers of the perithecial wall and in the flat-topped perithecia formed by the palisade of branched hyphae, which all terminate at the same level, surrounding the ostiole.

No asci and few ascospores were present in the type material and these are described from the collection by Petch. Berkeley and Broome gave the measurements of the ascospores as  $5-6.5\mu$ . This is the size of the conidia which they apparently mistook for the ascospores.

#### DESCRIPTION

The perithecia are scattered to gregarious on the stalks of cabbage and develop amongst a dense aggregation of *Gliocladium* sporodochia. The latter are presumed to be the conidial state and have a stalk  $100-123\mu$  long and  $100\mu$  broad formed

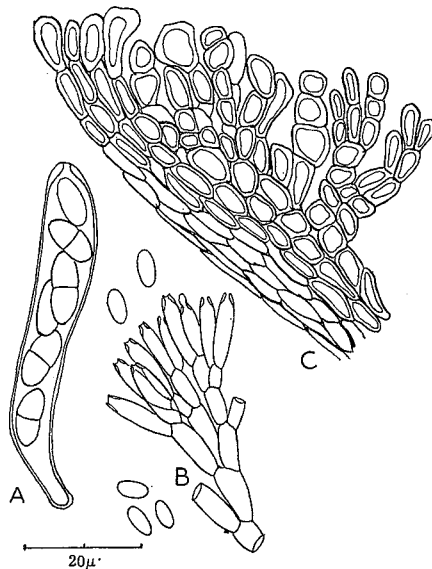


FIG. 11. *Nectria keithii*. A, ascus; B, associated conidia and conidiophores on host; C, part of perithecial wall near ostiole.

of tightly compressed parallel hyphae which separate apically and branch repeatedly to form the head. Each branch terminates in 2-3 metulae and these either bear 2 or more metulae at the apex, or 3-5 phialides. The phialides are hyaline, sub-doliform,  $10-12 \times 2-2.5\mu$ . Conidia formed from these cover the

sporodochium with a cream-coloured head; they are hyaline, oval, and measure  $5-7 \times 2-2.5 \mu$ .

The perithecia develop on a byssus or weakly developed pseudoparenchymatous stroma and are yellow to light brown in colour with a smooth or warty outer wall. They are oval to globose, with an apical collar surrounding the ostiole, and measure  $200-260 \mu$  in diameter. The collar is formed of shortly branched hyphae which terminate at the same level to form a flat-topped perithecium. In section the lateral wall is  $26-32 \mu$  wide and formed of two regions. The outer,  $12-15 \mu$  wide, is formed of thick-walled globose cells  $5-6 \mu$  in diameter. In the apical region these cells give rise to the processes surrounding the ostiole. The inner region is formed of elongated cells which show a gradation from the outer layers towards the centre, they measure  $8-10 \times 2 \mu$ .

The asci are clavate with a rounded apex bearing a central pore, they measure  $50-70 \times 7-10 \mu$ , and have 6-8 subdistichous ascospores.

The ascospores are ellipsoid to ovate, hyaline, smooth-walled, and measure  $8-12 \times 3.5-5 \mu$ .

## SPECIMENS EXAMINED

*Nectria keithii* folder Herb. R.B.G. Kew

*Nectria keithii* on cabbage (decorticated stems), Forres, Rev. J. Keith (Type coll.).

*Nectria subquaternata* folder (Brit. coll.) Herb. B.M. Nat. Hist.

On stalks of *Brassica*, North Wootton, T. Petch, Nov. 35.

*Nectria keithii* folder (Brit. coll.) Herb. B.M. Nat. Hist.

On cabbage stalks, Batheaston, Mar. 1877, C. E. Broome.

*Nectria keithii*

*Nectria solani* Reinke & Berthold, *Zersetzt d. Kartoffel*, p. 39, 1879.

Associated with the perithecia is a *Gliocladium* conidial state. Reinke and Berthold (1879) stated that they had grown this from the ascospores of *Nectria solani*. Although this has not been repeated to my knowledge, there is no reason to suspect that it is incorrect. Reinke and Berthold referred to it as *Spicaria solani* de Bary which Petch (1944) transferred to *Gliocladium solani* (Harting) Petch. As stated by Petch, loc. cit., de Bary took the name from Harting (1846). Although there is some doubt as to whether Reinke and Berthold had the correct *G. (Spicaria) solani* (see Brown and Smith 1957) there is little doubt that they had the correct conidial state of *N. solani*.

Unfortunately, Petch did not grow the ascospores of the collection made by Bramley in 1944 but the *Gliocladium* associated with these perithecia agrees with Reinke and Berthold's description and figures. In 1957 Mr. Bramley sent me a fresh collection of this *Gliocladium* on potato. This was isolated and cultured on a variety of media including sterilized potatoes and elm twigs. On the last two, perithecial-like bodies similar to those of *Nectria solani* developed, but unfortunately no asci or ascospores were formed. Thus, although not confirmed, the available evidence supports Reinke and Berthold's statements.

## DESCRIPTION

The perithecia form on a thick erumpent stroma which is formed of a mass of pulvinate yellow hyphae without pseudoparenchyma. The perithecia are obovoid to globose, yellowish brown with an opaque roughened outer wall and usually a short obtuse ostiolar papilla. They measure  $500-600\mu$  high and  $300-400\mu$  in diameter. In section the lateral wall is  $40-45\mu$  wide and formed of three

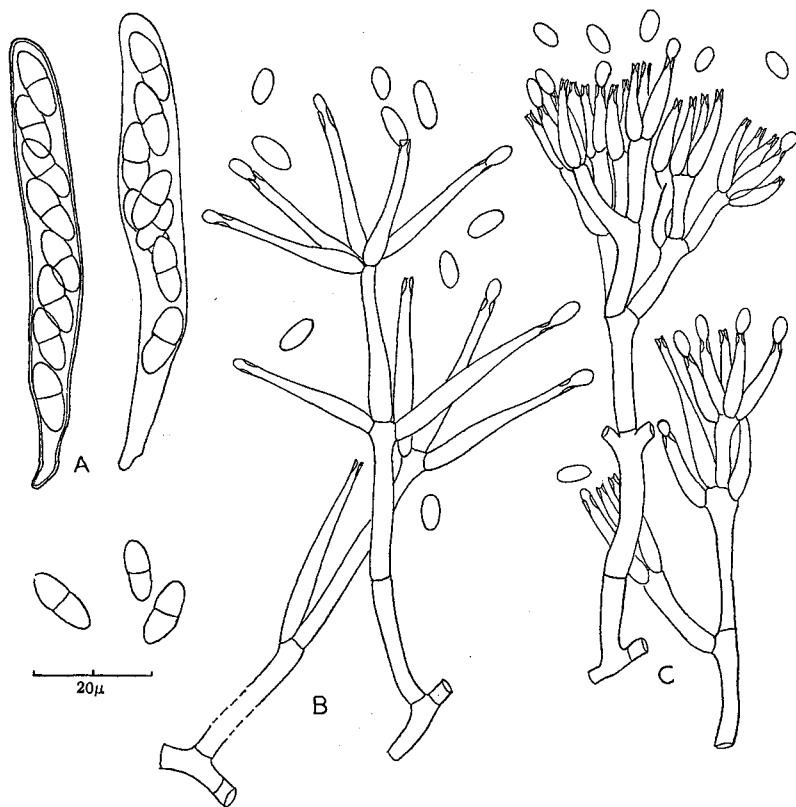


FIG. 12. *Nectria solani*. A, asci and ascospores; B, young conidiophores and conidia from culture; C, mature conidiophores and conidia.

regions. The outer is  $18-22\mu$  wide and composed of thin, yellow-walled, oval to hexagonal cells,  $10-16 \times 4-6\mu$ . The inner region has thin, yellow-walled, compressed cells,  $8-16 \times 1.5-2.5\mu$ . Lining the perithecial cavity are 3-5 layers of very thin-walled hyaline cells.

The asci are cylindrical to clavate with a thin rounded apex and obliquely monostichous to subdistichous ascospores, they measure  $60-75 \times 7-8\mu$ .

The ascospores are hyaline, broadly fusoid to ellipsoid, with a rough outer wall, when mature they measure  $10-14 \times 3.5-5\mu$ .

The *Gliocladium* conidial state associated with the perithecia has conidiophores formed of a stipe  $90-120\mu$  long and  $5-7\mu$  wide at the base. They branch once or twice towards the apex and each branch bears 2-5 metulae  $10-18 \times 3-3.5\mu$  with a swollen apex bearing a cluster of 3-8 phialides. These phialides



are hyaline obclavate with an apical collar and measure  $10-16 \times 2.5-3 \mu$ . They produce hyaline, ellipsoid to oval, aseptate conidia,  $5-7 \times 2.5-3 \mu$ .

#### CULTURES

Isolations of the conidia on potato dextrose or malt agar formed a colony of white floccose mycelium which covered the agar slope in about 14 days. The agar had a slight yellow discoloration. The conidiophores which soon cover the surface of the colony are formed of a simple erect stipe  $60-70 \mu$  long and  $4 \mu$  at the base narrowing to  $1.5-2 \mu$  at the apex. In the first-formed conidiophores the stipe terminates in a whorl of 4-6 phialides. Later-formed conidiophores are similar to those found on the host and have a branched apex forming a penicillate head. In these conidiophores, one of the metulae may grow through the phialide to form an extension to the stipe, and this bears a further penicillate head at a higher level.

The conidia are simple, cylindrical with rounded ends and may be slightly curved; they measure  $7-10 \times 2-3 \mu$ .

#### SPECIMENS EXAMINED

*Nectria solani* folder Herb. R.B.G. Kew

Libert, Herb. Jard. Bot. Bruxelles, 809, *Sphaeria* on *Solanum tuberosum*. In Brit. Coll. *Nectria solani*, Bolton Percy, Yorks., W.G.B., July 43.

*Nectria solani* folder Herb. I.M.I.

On potato, Bolton Percy, Yorks., W.G.B., May 43 (56769); Malton, Yorks., W.G.B., Sept. 57 (70653b).

#### THE COCCINEA AND MAMMOIDEA GROUPS

Typically the *Coccinea* group have red and semi-translucent perithecia when fresh. In section the wall is formed of thick-walled globose cells in the outer layers, and these merge into thinner-walled and more elongate cells in the inner layers.

The *Mammoidea* group on the other hand is typified by large reddish-brown perithecia that in section have the central region of the wall occupied by pseudo-palisade tissue. Outside this region one or more layers of large globose cells may or may not be present.

These perithecial characters are associated with distinct cultural characters. Thus *Nectria coccinea* has abundant microconidia followed several days later by macroconidia and then by perithecial initials that seldom mature in culture. Little discoloration of the agar is present. *N. mammoidea* has a complete absence of primary or microconidia, abundant macroconidia form in young cultures and these are followed in 10-14 days in the first isolates by abundant perithecia, the agar showing a strong purple coloration.

When all the species assigned to these two very distinct groups are considered it is found that *Nectria fockeliana* and *N. veuillotiana* have characters intermediate between the two. Thus *N. fockeliana* has a tendency towards the 'mammoidea' type of lateral wall, but as it forms abundant microconidia it is placed

in the 'coccinea' group. On the other hand, *N. veuillotiana* has almost a 'coccinea' type of wall but no microconidia and is therefore placed in the 'mammoidea' group.

### NECTRIA COCCINEA GROUP

This group is represented in Britain by *Nectria coccinea*, *N. fockeliana*, *N. punicea*, *N. ditissima*, *N. hederæ*, and *N. galligena*, and the variety *N. punicea* var. *ilicis*.

Perithecia in section show a simple wall structure which basically forms two regions. The outer region consists of globose cells with rather thick walls which are a continuation of the stroma; the cells forming the inner layers of this region may be smaller and more compact but do not form a distinct region. The second region is formed of the very thin-walled and elongated cells which line the perithecial cavity and represent the true perithecial wall. Species such as *Nectria fockeliana* show relationship with the *Mammoidea* group.

Asci are of two types; the first is clavate with distichous ascospores and no apical ring, these belong to the pathogenic series; the second have cylindrical asci with obliquely monostichous spores and an apical ring in the ascus.

Cultures are colourless becoming brownish as they dry out; microconidia are formed early and followed by macroconidia of the form genus *Cylindrocarpon*.

The species of this group have the widest literature and have been more frequently misdetermined than any other section of European *Nectrias*. This confusion has arisen because of the variability of *N. coccinea* itself and because of the heterogeneous collection of species to which the name was first applied. The extensive literature is due to the economic importance of *N. galligena* and some other species of this group as the causal organism of canker and die-back of hard-wood trees.

*Nectria coccinea* was first described by Persoon (1800 and 1801) as *Sphaeria coccinea*—caespitosa dilute rubra, sphaerulis ovatis laevibus—Hab. haud infrequens in cortice exsiccato Fagi sylvaticae.

The specimens in Persoon's herbarium labelled *Sphaeria coccinea* and those similarly named by Fries which have been examined by the writer are given below.

Label	Handwriting	Herb. & No.	Substrate	Present determination
<i>Sphaeria coccinea</i>	Persoon	Leiden 910, 270-56 <sup>1</sup>	<i>Fagus</i> bark	<i>N. coccinea</i> (Pers.) Fr.
66 <i>Sph. coccinea</i>	Muhlenberg	910, 270-58	Bark	<i>N. coryli</i> Fuekel
<i>Sphaeria coccinea</i> <i>laeta</i> Pers. S. 49- 92 <i>Abietina</i> Alb. & Schw.	Chaillet	910, 270-68	? <i>Abies</i> bark	<i>N. fockeliana</i>
12 <i>Sphaeria coccinea</i> <i>parasitica</i>	Persoon	910, 270-67	<i>Quaternaria</i> <i>quaternata</i> on <i>Fagus</i>	<i>N. episphaeria</i>
<i>Sphaeria coccinea</i> <i>S. coccinea</i>	Fries Printed	Uppsala Uppsala, Scler. Suec. 1813 <sup>2</sup>	Bark ? <i>Corylus</i>	<i>N. coccinea</i> <i>N. coryli</i>

<sup>1</sup> This specimen is selected as the lectotype of *N. coccinea*.

<sup>2</sup> The part of this exsiccatum in Herb. Kew is also *N. coryli*.

Because of the misdeterminations amongst these collections the first specimen cited from Persoon's herbarium, which also agrees with his description and figures (1798-1801), is taken as the lectotype of the species *Nectria coccinea* (Pers. ex Fr.) Fr.

Tulasne (1865) noted the confusion associated with the name *Nectria coccinea* and also noted that Fries (1849) had said that this species had elongate filiform ascospores (apparently a further confusion with *Scolecconectria cucurbitula*). It was because of this that Tulasne proposed the name *Nectria ditissima* 'to which', he said, 'belong in part the *Sphaeria coccinea* of most writers on mycology'. He cited the following exsiccata; Moug. & Nestl. Stirpes Vog. Rhen. No. 180, 1811; Desmazières, Pl. Crypt. Fr. fas. 8, No. 380, 1829. The parts of the latter examined by the writer are *N. coccinea*; those of the former are a collection of different species. However, collections made by Tulasne at Pierrefonds in 1857 and labelled by him as *N. ditissima* are a distinct species more closely allied to *N. galligena* than to *N. coccinea*; these are discussed later.

Great interest was aroused in the name *Nectria ditissima* when Hartig (1878) stated that it was the causal organism of canker on *Fagus*, *Quercus*, *Corylus*, and numerous other trees. This was also supported by Goethe (1880) working on the destructive canker of apple-trees, when he stated that he found it to be caused by a *Nectria* not significantly different from *N. ditissima*.

Appel and Wollenweber (1910) reporting inoculation experiments with organisms isolated from cankers on beech and apple, stated that they were the same species, namely *Fusarium wilkommii*, and that this must be conidial *Nectria ditissima*.

Weese (1911) said that *Nectria ditissima* was a synonym of *N. coccinea* and that this species did not cause canker and was in fact a saprophyte. The canker-causing *Nectria* was morphologically distinct and he identified this as *N. galligena* Bres.

This statement by Weese was not readily accepted by some contemporary workers, and Voges (1914) denied Weese's statement that *Nectria ditissima* was unable to cause canker. Wollenweber (1913) had already followed Weese and named his fungus *N. galligena*, at the same time proposing the form genus *Cylindrocarpon* for the conidial state and naming it *C. mali* (Allesch.) Wr.

Weese (1919), after examination of Voges' and Goethe's material, wrote that both men had in fact worked with *Nectria galligena* and not *N. ditissima*.

Similar confusion existed in the early nomenclature of the species *Nectria punicea* and *N. fuckeliana*. The former name was first used on a Rabenhorst Exs., No. 634 and this was found to be *N. cinnabarina*. *N. fuckeliana* is a new name for *N. cucurbitula* sensu Fuckel; this was a misdetermination of *Scolecconectria* [*Nectria*] *cucurbitula*. These are further discussed under the appropriate species.

Probably the most important paper to be published since Weese (1911) on this group was by Ashcroft (1934). Ashcroft agreed with Weese in considering that *Nectria galligena* was the canker-causing organism but he recognized Tulasne's collection of *N. ditissima* to be a distinct species, identical with the species which Ehrlich (1934) had found associated with beech bark disease. Ashcroft was reluctant to take up the name *N. ditissima* because he considered it a synonym of *N. coccinea*. Ashcroft used ascus and ascospore characters to

make a critical separation of the species. He found that this section of the wood-inhabiting *Nectria* spp. formed three groups, with the pathogenic species in the first group and the saprophytic species in the third; presumably the middle group was occupied by the weakly parasitic species. These groups were defined as follows:

#### GROUP I

Spores variable in size and shape, oval-elliptical, spindle-shaped or constricted; asci broadly clavate, usually two-ranked above; perithecia on smooth bark isolated or in small groups (2-5) on a common stroma.

#### GROUP II

Spores uniform in size and shape, oval; asci cylindrical or sometimes narrowly clavate and usually one-ranked, with the apex rounded and not extended beyond the topmost spore; perithecia on smooth bark grouped in large numbers (10-50) on a common stroma.

#### GROUP III

Spores uniform in size and shape, oval; asci cylindrical and usually one-ranked; with truncate or flattened apex usually extended somewhat above the topmost spore and provided with a distinct pore; perithecia grouped as in group II.

The following modified arrangement of these groups has been found applicable in separating the British species.

1. Asci clavate with thin undifferentiated apex. Spores, apically distichous even in young asci, are variable in size and shape, oval, elliptical or spindle-shaped.
  - a. Perithecia with rough walls in groups of 2-5 on common stroma . . . . . *N. galligena*
  - b. Perithecia with smooth 'varnished' walls, typically in groups of 5-30 . . . . . *N. ditissima*
  - c. Perithecia small, 230-250  $\mu$  dia. often crowded in groups of up to 100, walls smooth
    - Ascospores 11-17  $\times$  4-6  $\mu$ , on *Rhamnus* . . . . . *N. punicea*
    - Ascospores 16-24  $\times$  7-10  $\mu$ , on *Ilex* . . . . . *N. punicea*  
var. *ilicis*
2. Asci cylindrical with thickened apex bearing a 'chitinoid' ring. Spores obliquely monostichous but may be apically distichous in mature ascus. Spores uniform in size and shape, oval.
  - d. Perithecia 200-300  $\mu$  dia., scattered or aggregated on a weak stroma; on *Hedera helix* . . . . . *N. hederæ*
  - e. Perithecia 250-350  $\mu$  dia., scattered or in groups of 5-30 on a well developed stroma . . . . . *N. coccinea*
  - f. Perithecia 300-400  $\mu$  dia., in groups of 10-100 on a well developed stroma; on conifers . . . . . *N. fockeliana*

- Nectria coccinea* (Pers. ex Fr.) Fries, Summa Veg. Scand., ii, p. 388, 1849.  
*Sphaeria coccinea* Pers., Icon. & Deser. Fung., ii, p. 47, 1800; Syn. Meth. Fung., p. 49, 1801.  
*Sphaeria coccinea* Pers. ex Fr., Syst. Mycol., ii, p. 412, 1823.  
*Sphaeria decidua* Tode, Fung. Meckl., ii, p. 31, 1791 (teste Fries loc. cit.).  
*Cucurbitaria coccinea* (Pers.) S. F. Gray, Nat. Arrang. Brit. Pl., i, p. 519, 1821.  
*Creonectria coccinea* (Pers. ex Fr.) Seaver, *Mycologia*, i, p. 188, 1909.

The following diagnosis given by Fries (1823) followed closely Persoon's original description in 1800:

*Sphaeria coccinea*, caespitosa, peritheciis ovatis laevibus laete rubris, ostiolo papillaeformi.

Although this is basically correct it is somewhat inadequate. In fact, the species limits of *Nectria coccinea* have been extremely difficult to determine. Over 100 collections have been examined and ascospore isolations made from twenty-two. Typically, perithecia form in groups of 5-35 on a common stroma that forms in the cortex. When perithecia develop on bare wood they are often solitary, scattered, and without a stroma.

The stroma is 0.5-1.5 mm. in diameter when it forms in a compacted cortex like *Fagus* or *Taxus*. It is pseudoparenchymatic and composed of elongate cells 14-23 × 7-10  $\mu$ . On a softer or looser periderm like *Tilia* the stroma is only pseudoparenchymatic below the perithecia. In the host tissue it is represented by a web of mycelium in which the individual hyphae are clearly visible.

The perithecia are oval to ovate or even sub-globose, but with a short-pointed ostiolar papilla usually darker than the rest of the perithecium. When young, they are bright red, and appear translucent when fresh, but become rougher and darker with age; they measure 250-350  $\mu$  in diameter.

In section, the lateral wall is 35-45  $\mu$  wide and shows a gradation from the thick-walled globose cells 7-12  $\mu$  diameter of the outer layers, to the thinner-walled and more elongate cells 7-12 × 5-6  $\mu$  of the inner layers. Lining this principle wall region are several layers of hexagonal, very thin-walled cells that are crushed in the mature perithecium.

The asci are cylindrical with a rounded apex containing a central pore, they measure 75-100 × 7-10  $\mu$ . Ascospores are at first monostichous and form some distance back from the tip of the ascus but when mature they are obliquely monostichous or apically subdistichous and move up to the apex.

Ascospores are ellipsoid and slightly constricted at the central septum. They are fairly even in size and shape, hyaline becoming very light brown, and may be slightly verrucose at maturity; they measure 12-15 × 5-6  $\mu$  (10-17 × 4-7  $\mu$ ).

#### CULTURES

Ascospores germinate readily, forming hyphal primordia from the apex of each cell of the spore and later from one or more points in the lateral wall. In single-spore isolations the mycelium covers the surface of the agar slope in a test-tube in 2-3 weeks. On potato dextrose agar this may be thick, floccose or fibrous, yellowish white to grey. A yellowish-brown discoloration of the agar forms in 3-4 weeks and this gradually changes to chocolate brown in older

cultures. In approximately 4 weeks, reddish-brown stromatic pustules form at the edge of the agar.

Microconidia form after a few days, at first on simple lateral phialides on the

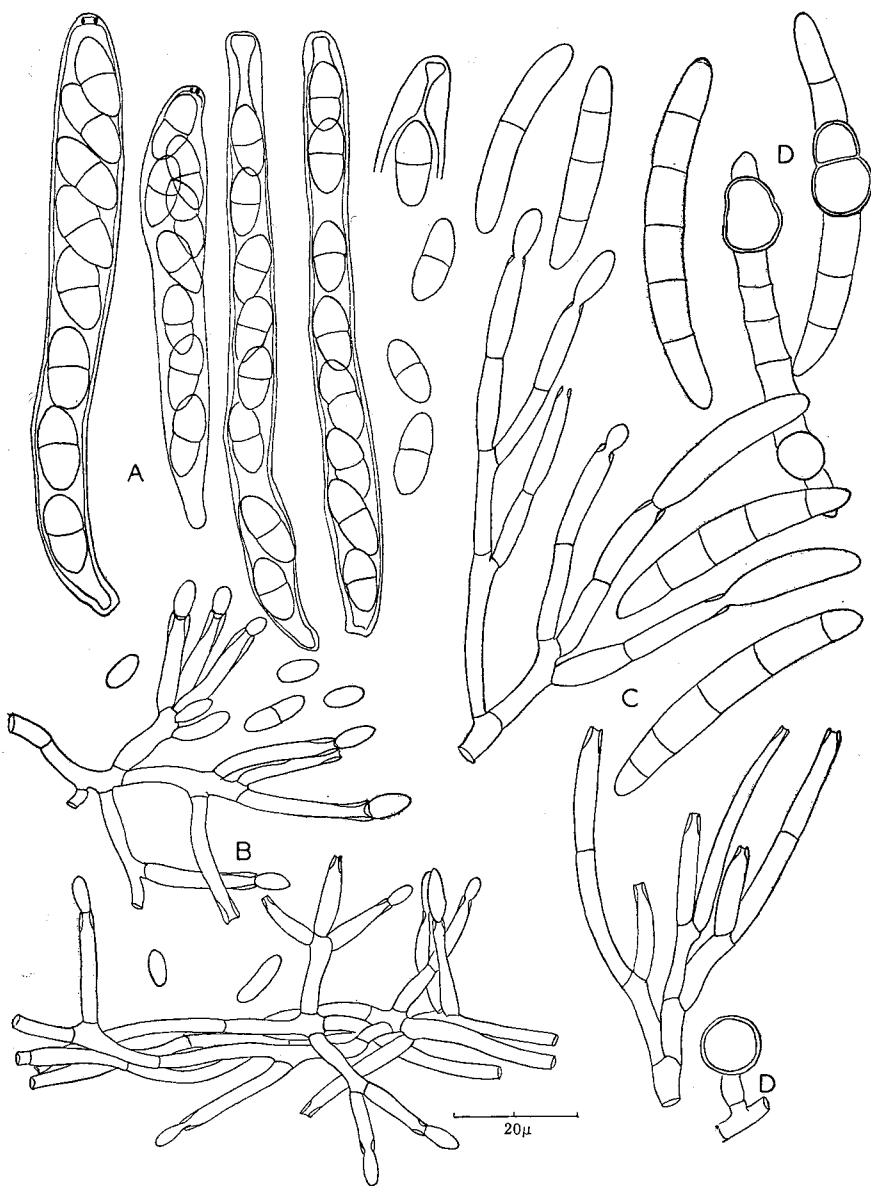


FIG. 13. *Nectria coccinea*. A, asci and ascospores; B, microconidiophores and conidia; C, macroconidiophores and conidia; D, chlamydospores.

hyphae, but in older cultures as terminations to the branches of the conidiophores; or 3-4 phialides may form a whorl at each septum of the conidiophore. The phialides are almost cylindrical but narrow slightly towards the apical collar; they measure 9-20  $\mu$  long and 1.5-2.5  $\mu$  at the base. Microconidia are

4-9 × 1.5-3 μ, hyaline, cylindrical with rounded ends and occasionally slightly curved.

Macroconidia begin to form in 3-4 weeks from phialides that occur as terminations to dicotomously branched conidiophores. These phialides are broader than the primary ones and measure 12-20 × 3-5 μ. *Cylindrocarpon* macroconidia are hyaline, cylindrical, narrowing slightly towards the apex and a smaller amount towards the base, when mature they have 3-7 septa and measure:

0-septate	20-36 × 5 μ
1-septate	30-40 × 5 μ
2-septate	34-46 × 6 μ
3-septate	46-60 × 6-7 μ
4- or more septate	50-80 × 6-7 μ

## SPECIMENS EXAMINED

Ex Herb. Pers. Herb. Lugd. Bat.

*Sphaeria coccinea* Pers. No. 910, 270-56 on *Fagus* bark (lecto-type).

Ex Herb. Fries Botaniska Mus. Uppsala

*Sphaeria coccinea* (scripsit Fries) on bark.

*Nectria coccinea* folder in Herb. R.B.G. Kew

C. Roumeguère, Fung. Gall. Exs. 272, 981, 890, 1643; Herb. Barbey-boissier 859 (Fung. Rhen. 980); M. A. Libert, Pl. Crypt. Ard. 242; P. A. Saccardo, Mycoth. Veneta 97; Desmazières, Crypt. Fr. 380 and 777; J. E. Vize, Micro-Fung. Brit. 152; M. C. Cooke, Fung. Brit. Exs. 494 and 562; Thümen, Mycoth. Univ. 1063; Plowright, Brit. Exs. 8; Rabenhorst, Fung. Europaei 1630; Sydow, Myco. Mar. 1717; Baxter, Stirp. Crypt. Oxon. 25 (as *Cucurbitaria*).

*Nectria coccinea* folder Herb. I.M.I.

One collection only is cited for each host. The species is most frequently found on *Fagus*.

On *Acer*, Selworthy Woods, Somerset, R. McAleer, May 57 (60246). On *Alder*, Mulgrave Woods, Yorks., S.J.H., Sept. 46 (6897). On *Betula*, Ashridge Park, Herts., C.B. May 55 (60246). On *Carpinus*, Blaze Woods, Bristol, J.W., Sept. 55 (61044a). On *Castanea*, nr. Birmingham, E.W.M., (22845). On *Corylus*, Kingthorpe, Yorks., W.G.B., May 57 (69082). On *Fagus*, Clapham, Yorks., W.G.B., Sept. 57 (70655). On *Fraxinus*, Ribston Park, Yorks., C.B., April 58 (72791). On *Hedera*, Beesands, Devon, C.B., Aug. 54 (56914). On *Ilex*, Ranmore Common, Surrey, C.B., Mar. 58 (72171a). On *Morus*, Stratton Strawless Woods, Norfolk, E.W.M., Oct. 34 (51590). On *Populus*, Pickering, Yorks., W.G.B., Jan. 56 (61855). On *Quercus*, Mulgrave Woods, Yorks., S.J.H., Sept. 46 (6899). On *Rhamnus*, Marysville, Wash., U.S.A., J. M. Grant, Mar. 27 (26626). On *Sambucus*, Wheatfen Broad, Norfolk, E.A.E., Dec. 55 (62102). On *Taxus*, Ranmore Common, Surrey, C.B., Nov. 57 (71041). On *Tilia*, Hawes, Yorks., W.G.B., Sept. 57 (70654). On *Ulmus*, C.M.I., Surrey, E.W.M., July 31 (22846).

*Incorrectly named Exsiccata* in *Nectria coccinea* folder, Herb. R.B.G. Kew

C. Roumeguère, Fung. Gall. Exs. 980 *Nectria coccinea* = *N. cinnabarina*

J. B. Desmazières, Pl. Crypt. 1757 *Sph. coccinea* var. *cicatricum* = *N. desmazieri*

H. W. Ravenel, Fung. Amer. Exs. 737 *Nectria coccinea* = *N. episphaeria*

P. A. Karsten, F.F. exs. 167 *Nectria coccinea* = *N. fuckeliana*

E. Fries, Scler. Suec. 183 *S. coccinea* = *N. coryli*

P. Sydow, Mycoth. March. 2431 *Nectria coccinea* = *N. cinnabarina*

*NECTRIA GALLIGENA* AND *NECTRIA DITISSIMA*

Some account has already been given of the confusion between *Nectria galligena* and *N. ditissima* and their relationship to the parasitic cankers on hardwood trees. When Hartig, (1878) and later Goethe (1880) found the causal organism to be a *Nectria*, both suggested that it was *N. ditissima* Tul. It was not until 1911 that Weese wrote that *N. ditissima* was a synonym of *N. coccinea* and that the canker-causing organism was *N. galligena*.

The question was reopened by Westerdijk and Luijk (1924) when they found a small-spored *Nectria* corresponding to *N. coccinea* causing canker of poplar. This was identified for them by Weese as *N. coccinea*, although it should be mentioned that Weese was not entirely satisfied with his own determination of this fungus. Westerdijk and Luijk showed this species to be pathogenic on apple, beech, and poplar and this led these two workers to re-examine the evidence for the separation of *N. galligena* and *N. coccinea*. After stating that the only characters of value, amongst those used by Weese, were the larger ascospores of *N. galligena*, they said the species could only be separated by careful measurement of a large number of ascospores. The mean value of the ascospores of *N. galligena* would be found to be above  $15.9\ \mu$  long, whereas *N. coccinea* would have a mean value not above  $13.4\ \mu$ .

Wollenweber (1924) revived the name *Nectria ditissima* Tul. and used *Cylindrocarpon (Fusarium) wilkommii* as the name for the conidial state. He said that it was pathogenic on deciduous trees and distinct from *N. coccinea*. He also proposed the varieties *N. ditissima* var. *major* Wr. and *N. ditissima* var. *artica* Wr. and recognized *N. galligena* var. *major* as a variety on ash of *N. galligena*.

Richter (1928), who had worked under Wollenweber's direction, published the distinguishing characters by which these varieties could be separated.

Ashcroft (1934) could find no validity in either Westerdijk's and Luijk's separation or that proposed by Richter. In fact, he considered that Wollenweber's varieties of *Nectria ditissima* and *N. galligena* had no validity whatever and that the canker-causing organism was one species, namely *N. galligena* Bres. However, the species which Ehrlich (1934) had shown to be associated with the beech-bark disease and dieback in Nova Scotia and which the writer finds identical with Tulasne's collection of *N. ditissima*, was separated by Ashcroft as a distinct species. Ashcroft was reluctant to take up the name *N. ditissima* as he considered it to be a synonym of *N. coccinea*. As Wollenweber had already re-established the species and shown that it could be easily separated from both *N. galligena* and *N. coccinea* on the micro- and macroconidia in culture the name is used here. I also find that it can be separated from *N. galligena* on its perithecial appearance and formation, and from *N. coccinea* on the ascus structure.

*Nectria galligena* Bresadola in Strasser, *Verh. K. K. Zool. Bot. Ges. Wien*, li, p. 413, 1901.

*Nectria ditissima* Tul. f. *salicicola* Rehm, *Asc. Exs.*, xxvii, No. 1345, 1900.



*Nectria galligena* var. *major* Wollenw., *Angew. Bot.*, viii, pp. 189, 200-1, 1926.

*Fusarium mali* Allesch. *Ber. bot. Ver. Landshüt.*, xii, p. 130, 1892.

*Cylindrocarpon mali* (Allesch.) Wollenw., *Z. Parasitenk.*, 1, p. 150, 1928.

*Cylindrocarpon mali* var. *flavum* Wollenw., *Z. Parasitenk.*, 1, p. 150, 1928.

I have been unable to find any morphological evidence for separating *Nectria galligena* on *Fraxinus* as a variety. If it can be shown that this fungus is incapable of causing canker of apple then it should be referred to as a *forma specialis*.

#### DESCRIPTION

Perithecia on, or associated with, brown usually fissured cankers on the branches of deciduous trees.

Before and during perithecial formation, conidial pustules are usually formed on the surface or edge of the canker. These conidia are cylindrical, slightly curved, and narrowing towards each end. The upper ends are rounded and the base slightly flattened, they measure  $55-65 \times 5-6 \mu$ .

Perithecia are scattered to gregarious, bright red, ovate or occasionally globose, with a smooth wall when young, but becoming darker and more warted when they mature, they measure  $250-350 \mu$  in diameter. The ostiolar disc is slightly convex and darker than the venter. In section the lateral wall is  $40-60 \mu$  wide depending on the state of maturity. It is formed of three regions, although there is no clear distinction between the two outer ones. The outer layers of cells are oval to globose,  $6-9 \times 4-8 \mu$  and these merge into the more elongate cells  $14-18 \times 3-4 \mu$  of the middle region. The inner region is formed of elongate and very thin-walled cells which become crushed as the perithecium matures. Paraphyses are abundant and persist until the asci mature.

The asci are clavate with a thin wall and with 5-8 obliquely monostichous or apically distichous ascospores, they measure  $75-95 \times 12-15 \mu$ .

Ascospores are variable in shape and size, in a single mature ascus they may be oval, ellipsoid, or spindle-shaped and slightly constricted at the central septum; they are hyaline, smooth to slightly verrucose, and measure  $14-22 \times 6-9 \mu$ .

#### CULTURES

Single ascospores isolated on to malt and potato dextrose agar in test-tubes covered the surface of the slope with a white floccose mycelium in 2-3 weeks. Microconidia forming on the surface and at the edge of the mycelial mat are cylindrical with rounded ends, aseptate  $4-8 \times 2-3 \mu$ . Macroconidia tend to form as pustules from multi-branched conidiophores. Each branch of the conidiophore terminates in a phialide  $12-16 \mu$  long and  $2-2.5 \mu$  at the base narrowing slightly towards the apex which has a thickening of the lateral wall to form a collar. Macroconidia are similar to those found on the host and measure:

1-septate	$10-28 \times 4-5 \mu$
2-septate	$28-30 \times 4-5 \mu$
3-septate	$36-47 \times 4-6.5 \mu$
4- or more septate	$47-65 \times 5-7 \mu$

A greenish-yellow discoloration developed in the agar after 3-4 weeks and

this became reddish brown as the media dried out. Perithecia formed sparsely in older cultures.

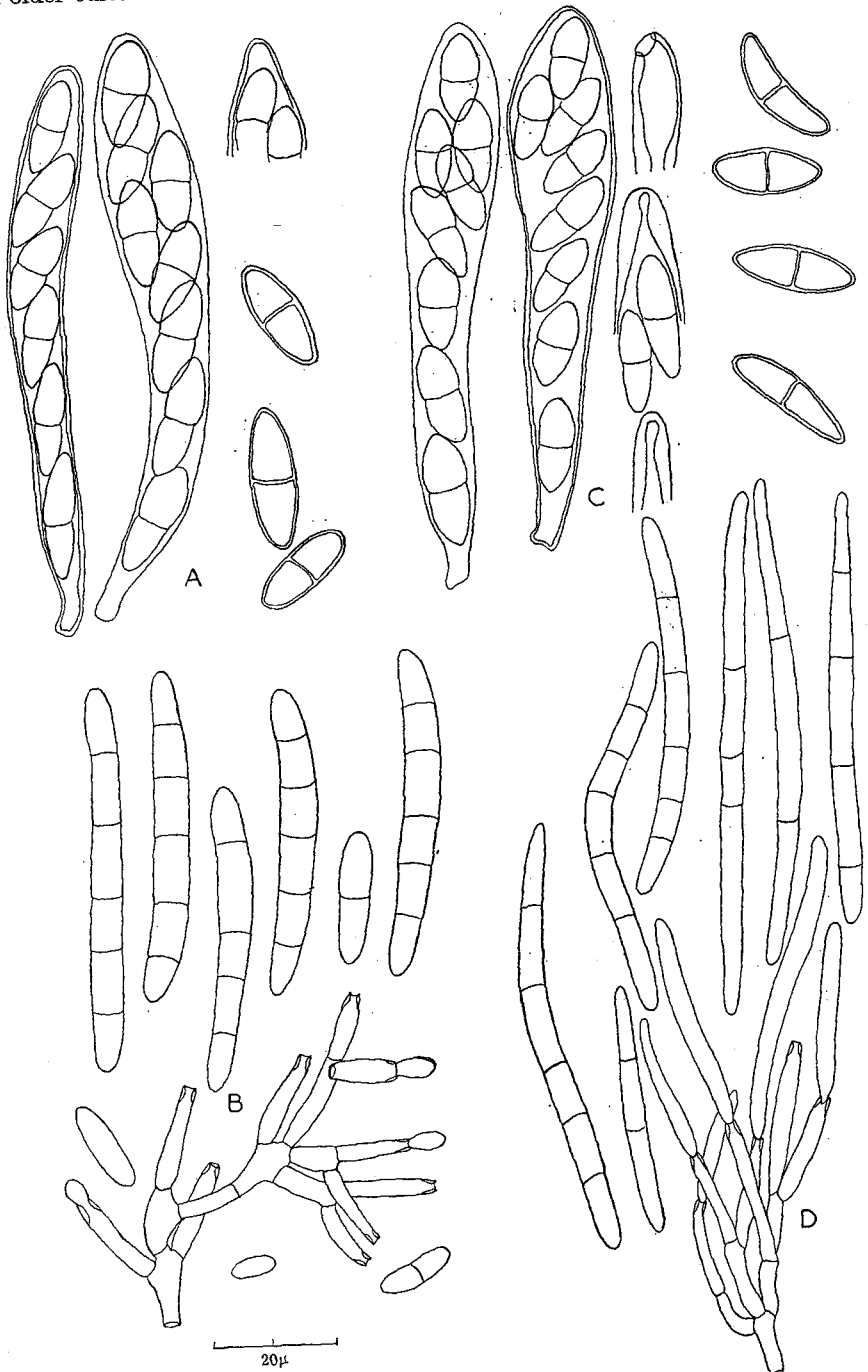


FIG. 14. *Nectria galligena*. A, asci and ascospores; B, microconidia and conidiophores and macroconidia. *Nectria ditissima*. C, asci and ascospores; D, macroconidia and conidiophores.

## SPECIMENS EXAMINED

*Nectria galligena* ex Herb. Mus. Bat. Stockholm

*Nectria galligena* Bres. (ex Herb. Rehm) Auf gallen am *Salix purpurea* am Sonntagsberg, 22.5.1907, P. Strasser.

*Nectria galligena* folder Herb. I.M.I.

On *Acer*, Little Compton, Rhode Island, U.S.A., J. H. Faull, Oct. 35 (52210). On *Aesculus*, Little Compton, Rhode Island, U.S.A., J. H. Faull, Oct. 35 (57218). On *Betula*, Worcester, Mass., U.S.A., J.E., Aug. 39 (52211). On *Carya*, Circa Syracuse, N.Y., H. F. A. Meier, 34 (52208). On *Fraxinus*, Lench Woods, Warwick, A. H. R. Buller, Sept. 33 (52195); Brantham Court, Suffolk, J.E., Oct. 33 (52198); Tring, Bucks., E.W.M. & J.E., Nov. 33 (52212); Sjaelland, Denmark, J.E., May 34 (52213); Glentress Forest, Peebles, Scotland, J.E. & M. Wilson, Mar. 35 (52214); Benmore Estate, Argyllshire, Scotland, J.E. & C. G. C. Chesters, Mar. 35 (52215); Ranmore Common, Surrey, E.W.M., Feb. 36 (22825); Wheatfen Broad, Norfolk, E.A.E., Mar. 47 (12280); Presteign, Radnorshire, J. Dingley, Sept. 57 (70660). On *Pyrus*, North Wootton, Norfolk, T. Petch, Feb. 25 (22824); Malone Road, Belfast, A. E. Muskett, ? Sept. 30 (52197); Sevenoaks, Kent, S. P. Wiltshire, June 33 (52196); East Malling, Kent, F. Hammond, Oct. 33 (52199); Cambridge, W. Dillon-Weston, Nov. 33 (52200); Mickleton, Gloucs., L. Ogilvie, Nov. 33 (52201); Jaegersborg, Denmark, J.E. & N. F. Buchwald, April 34 (52205); Baarn, Holland, J.E. & J. Westerdijk, June 34 (52206); Solihull, Birmingham, C. G. C. Chesters, Jan. 35 (22823); Auckland, N.Z., P. Fry, July 49 (50390); East Malling Res. Stat., Kent, M. H. Moore, Oct. 57 and Mar. 58 (70791 and 72477); on *Salix*, Windsor, Berks., J.E., July 34 (22823); Sonntagsberg, Austria, P. Strasser, Oct. 01 (22189); Vindobon Krypt. Exs. 613 (22187). These last two are taken as authentic for the name.

✓  
*Nectria ditissima* Tul., Selecta Fung. Carp. iii, 73-75, 1865.

## DESCRIPTION

Perithecia associated with 'die-back' or canker of *Fagus*. They occur in groups of 5-30 on a poorly developed stroma that is barely erumpent through the periderm. The perithecia are ovate to globose, yellow, becoming deep red and slightly darker round the ostiole, they have a smooth wall and measure 250-300  $\mu$  in diameter. In section, the lateral wall is 45-55  $\mu$  wide and formed of three indistinct regions. The outer, 20-24  $\mu$  wide, is composed of thick-walled globose cells 5-6  $\mu$  in diameter and interspersed with flattened cells 4-6  $\times$  2-3  $\mu$ . The central region has thinner-walled and more elongate cells 8-12  $\times$  3-4  $\mu$ . The inner region is formed of very thin-walled elongate cells that line the perithecial cavity.

The asci are clavate with a short stalk and rounded at the apex, without a ring and with eight subdistichous ascospores; they measure 85-95  $\times$  15-18  $\mu$ .

Ascospores are variable in shape and size, oval to ellipsoid and slightly constricted at the central septum, they measure 14-21  $\times$  5-8  $\mu$  (mean 16.9  $\times$  6.45  $\mu$ ). Tulasne's material examined by me was immature and the mean ascospore measurement was 12.6  $\times$  5.9  $\mu$ . Ashcroft gave a mean of the Tulasne material measured by him as 13.44  $\times$  6.07  $\mu$ .

## CULTURES

Single ascospores isolated on to malt, potato dextrose, and potato starch agar showed identical growth. In 14 days the colonies were white floccose, 1.5–2.5 cm. down the agar slope in a test-tube; a yellowish-green discoloration was present on the surface of the agar. Spore production was sparse although microconidia were formed on potato dextrose agar and both micro and macroconidia were formed on malt agar.

The microconidia were formed on short lateral pegs on the superficial hyphae, they were hyaline, oblong to allantoid,  $2-2.5 \times 0.8-1 \mu$ .

Macroconidia are formed on branched conidiophores, each branch terminating in 1–3 phialides. These are cylindrical, with a thickening of the lateral wall near the apex to form a collar, and they measure  $15-25 \times 2-3 \mu$ . Macroconidia are cylindrical, straight or slightly curved and narrowing somewhat towards the apex, they are 4–7 septate when mature and measure:

4-septate	$50-65 \times 3-5 \mu$
5-septate	$68-80 \times 4-5 \mu$
6-septate	$75-86 \times 5-6 \mu$
7-septate	$82-90 \times 5-6 \mu$

Perithecial initials formed in large numbers on all media as it began to dry out but no ascospores were found.

## SPECIMENS EXAMINED

Herb. Mus. Paris (Lab. Crypt.) Ex. Herb. Tulasne

*Nectria ditissima* in Fago, Pierrefonds, 1857 (slides of sections and spores) ex. Herb. Erhlich.

*Nectria ditissima* folder Herb. I.M.I.

On *Fagus*, Mark Brandenburg, Germany, J.E. & H. W. Wollenweber, May 34 (22822); Kenmore, Ireland, P. O'Connor, Dec. 34 (16979); Benmore Estate, Argyll; Crieff and Braco, Perthshire, Scotland, J.E. & C. G. C. Chesters, Mar. 35 (52216 & 22821); Westbury Forest, Hants, J. S. Murray, Mar. 58 (72302 & 72303), Oct. 58 (75242).

*Nectria punicea* (Schmidt ex Fr.) Fr. ex Rabenh., Herb. Myc., vii, No. 634, 1858.

*Sphaeria punicea* Schmidt in P. Kunze & Schmidt, Myk. Hefte i, p. 61, 1817.

*Sphaeria punicea* Schmidt ex Fr., Syst. Mycol., ii, p. 415, 1823.

*Nectria punicea* (Schmidt ex Fr.) Fuckel, Symb. Myc., p. 180, 1870.

*Nectria punicea* (Schm. ex Fr.) Fr. in Sacc., *Syll. Fung.*, p. 480, 1883.

Fries (1849) recognized the fungus as a *Nectria* but as he believed it to be exotic for the Scandinavian countries, it was not included in his list of *Nectria* species. The name was first published by Rabenhorst, loc. cit. Unfortunately, Rabenhorst misidentified the fungus and this exsiccatum, or at least the part in Herb. Kew, is *N. cinnabarina*. Cooke (1866) stated that he found this specimen indistinguishable from *N. cinnabarina* on *Ribes* and Rabenhorst (1866) believed it not sufficiently distinct from *N. cinnabarina* to justify its separation as a distinct species. Thus the frequent confusion between *N. punicea* and *N. cinna-*

*barina* on *Rhamnus frangula* has its origin in this exsiccatum. This would also account for the conidial state of *N. punicea* being cited as a *Tubercularia* (Petch, 1938). On other hosts, the confusion seems to lie between *N. punicea* and *N. coccinea*, and a list is given at the end of the misidentified collections amongst the exsiccata examined by the author.

The only British collections seen were made by Cooke on *Rhamnus frangula* and issued by him as Fung. Brit. No. 370 and No. 475. Also in Cooke's herbarium in Herb. Kew there are several other collections by him from Highgate.

Although this species has not been grown by the author, its conidial state has been fully described by Wollenweber (1926) and Richter (1928).

In Britain, the name *Nectria punicea* has been frequently used for a closely related fungus on *Ilex aquifolium*. This has been isolated several times by the writer and on comparison with Wollenweber's and Richter's description is sufficiently distinct to be taken as a variety of *N. punicea*.

	<i>N. punicea</i>	<i>N. punicea</i> var. <i>ilicis</i>
Ascospores	Obliquely monostichous Smooth walled	Sub-distichous Rough walled when mature
Microconidia	11.5-17 × 4-6 μ	14-24 × 7-10 μ
Macroconidia	5.5-11.5 × 2.5-4 μ	7.5-16 × 2.5-4 μ
	80-117 × 5-6 μ	90-115 × 6-8 μ

## DESCRIPTION

Perithecia crowded on an erumpent stroma 2.5-3 mm. dia. which bursts through the periderm of the host, they are ovoid to narrowly globose with a pointed ostiolar papilla, reddish-brown in colour with a smooth wall and measure 300-400 μ in diameter. In section the lateral wall is 60-70 μ wide and formed of two regions. The outer consists of thick-walled globose cells which show a gradation in size from 10-12 × 6-7 μ in the outer layers to 5-7 × 3-4 μ in the inner layers. The inner region 12-16 μ is formed of 5-6 layers of very thin-walled elongate cells which become compressed as the perithecium matures.

The asci are clavate, without an apical collar and measure 90-120 × 11-13 μ. The eight obliquely monostichous to sub-distichous ascospores are broadly fusoid to ellipsoid, hyaline with a smooth wall and slightly constricted at the central septum, they measure 14-16 × 6 μ.

## SPECIMENS EXAMINED

*Nectria punicea* folder Herb. R.B.G. Kew

Cooke, Fung. Brit. exs. 370 & 475; Fuckel, Fung. Rhen. 984; Westerndorp, Herb. Crypt. Belg. 1109 (2 pts); Herb. K. Starcs, Riga, Latvia, 873; *Nectria punicea* on *Rhamnus frangula*, Bishops Wood, Feb. 1866, ex Herb. Cooke, Kew.

*Nectria punicea* folder Herb. I.M.I.

On *Rhamnus frangula*, Fung. Brit., M. C. Cooke 475 (18366); F. Petrak, Mycoth. generalis, 475 (30357); A. Ludwig, Flora Westfalen (22180); Ex. Herb. K. Starcs 873 (22839); Vindobon Krypt. Exs. 821 (11400); Softeland, Bergen, Norway, Wollenw. 2001 (51939); Machnower Busch, Berlin, Germany, Wollenw. 2070/71 (51937).

INCORRECTLY NAMED EXSICCATA IN HERB. R.B.G. KEW OF *NECTRIA PUNICEA*

Libert, Herb. du Jardin Bot. Bruxelles, No. 678, 679, 680, 681 *Nectria punicea* all *N. cinnabarina*. Rehm, Ascomyceten 3371 *N. punicea* non est. De Thümen, Mycotheca universalis 1549 *N. punicea*, ?*N. cinnabarina*; Plowright, Sphaeria Brit. *N. punicea* = *N. cinnabarina*; Rabenh. Herb. Mycol. 634 *N. punicea* = *N. cinnabarina*; C. Roumeguère, Fung. Gall. Exs. 1465, 1646, & 1657 *N. punicea*, all = *N. cinnabarina*; Sydow, Myco. Marchia 1250 *N. punicea* = *N. cinnabarina*.

In Herb. I.M.I.

F. Petrak, 1930 (22181) *N. punicea* = *N. cinnabarina*.

*Nectria punicea* (Schm. ex. Fr.) Fr. var. *ilicis* var. nov. A Typo differt:

Asci 110–130 × 14–15  $\mu$ ; Ascospores distichae, 16–24 × 7–10  $\mu$ ; Macroconidia 90–115 × 6–8  $\mu$ .

Habitat in ramis *Ilicis aquifolii*. Typus, Llanrwst, N. Wales (I.M.I. 73437).

This variety is erected on the evidence outlined in the introduction to the previous species. It has a characteristic habitat and is common in this country. Its perithecia are found on the trunk or larger branches of dying or dead holly trees, often above the stroma of *Diatrype stigma*. The scattered perithecial stroma may reach from ground level to twenty feet or more up the trunk.

The perithecia are densely crowded and develop in succession on an erumpent stroma formed of homogeneous globose thin-walled cells 7–10  $\mu$  in diameter. The base of the stroma penetrates the lenticels and is usually only attached to the host by this narrow wedge of tissue. The perithecia are red to reddish brown, globose to ovate with a small apical disc and measure 230–250  $\mu$  in diameter. The outer wall is usually smooth and in section is 45–50  $\mu$  wide and composed of three indistinct regions. The outer is formed of cells that only differ from those of the stroma in having thicker walls, these cells are globose and measure 6–8  $\mu$  in diameter with a few 8–9 × 4–5  $\mu$ . The middle region has a yellow coloration with thinner-walled, globose to slightly elongate cells; apically this layer forms the disc. The inner region is formed of thin-walled elongate hyaline cells.

The asci are clavate with a rounded apex and eight monostichous to apically distichous ascospores, they measure 110–130 × 14–15  $\mu$ .

The ascospores are hyaline, broadly fusoid with a slight constriction at the central septum; usually the eight ascospores show considerable variation in size and shape in each ascus. When the spores are mature the walls are slightly roughened and light brown; they measure 14–24 × 7–10  $\mu$ .

## CULTURES

Ascospores germinate readily, and on malt or potato dextrose agar, the colonies are 1 cm. dia., white floccose and rather erumpent at the point of inoculum, after 7 days; primary conidia are present in abundance and secondary conidia just beginning to form. On malt agar the growth gradually assumes a sparse hairy appearance and after 4–5 weeks the agar becomes reddish brown. This discoloration is less marked on potato dextrose agar and also the aerial hyphae remain white and floccose. Macroconidia form as small pustules in older cultures.

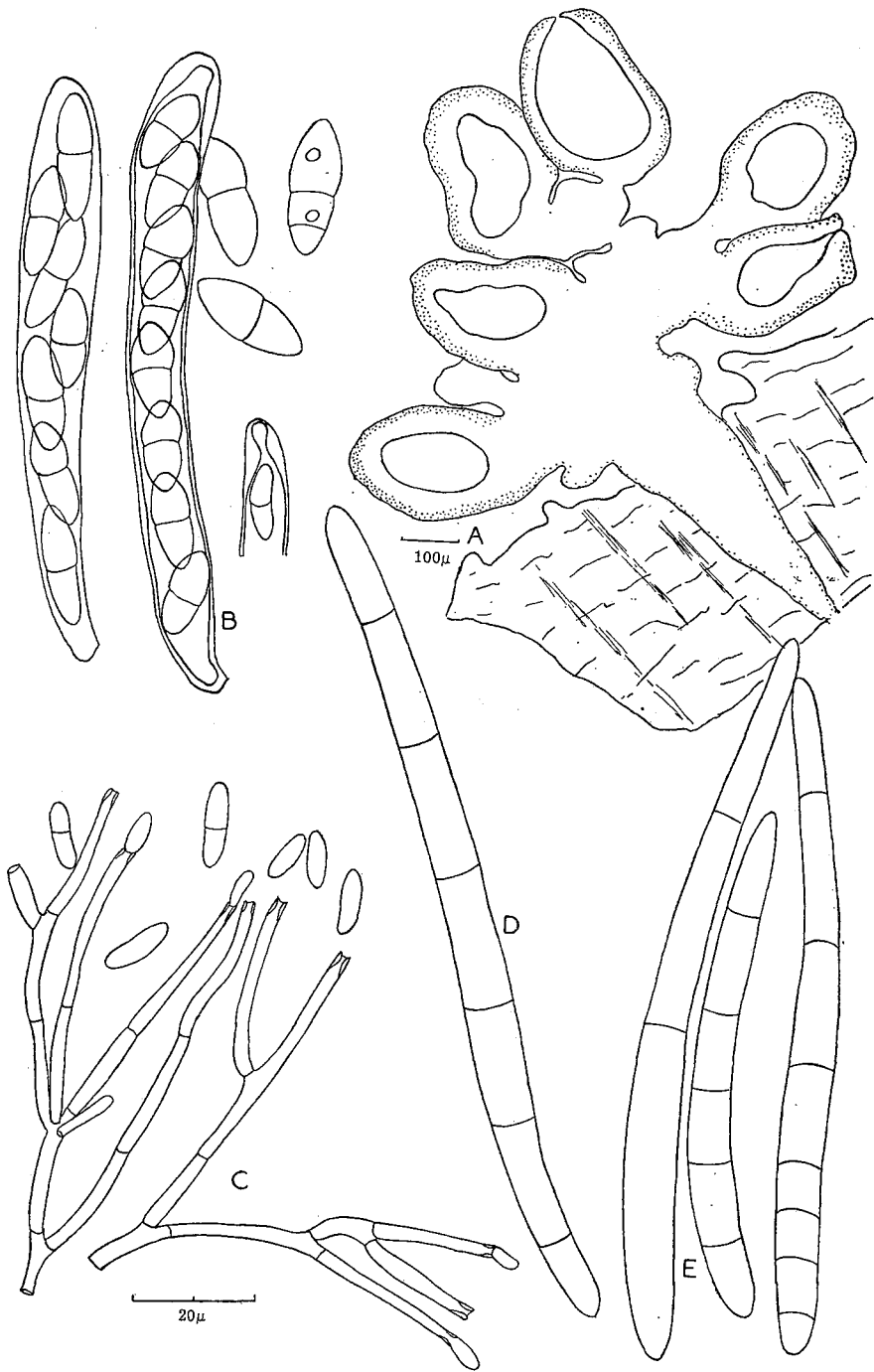


FIG. 15. *Nectria punicea* var. *ilicis*. A, diagrammatic section of perithecial stroma; B, asci and ascospores; C, microconidiophores and conidia; D-E, macroconidia; D, from host; E, from culture.

Microconidia form on lateral phialides, these may be simple (formed on the hyphae) or as terminations to short lateral branches. The phialides are 17–25  $\mu$  long and 2–2.5  $\mu$  at the base narrowing slightly towards the apex where they terminate in a collar. Microconidia are 7.5–16  $\times$  2.5–4  $\mu$ , hyaline, ellipsoid to cylindrical, and may become 1-septate.

Macroconidia develop sparsely, although more abundantly on malt than potato dextrose agar. They arise from short phialides that measure 18–32  $\times$  2.5–3.5  $\mu$ . The first to form are on simple conidiophores but in older cultures the conidiophores undergo repeated branching, and each branch terminates in a phialide. Macroconidia are cylindrocarpon-like, narrowing slightly towards the rounded ends. The greatest width of the spore is approximately one-third from the base. When mature they are 7–9 septate and measure 90–115  $\times$  6–8  $\mu$ .

#### SPECIMENS EXAMINED

*Nectria punicea* folder (Brit. coll.) Herb. R.B.G. Kew

On *Ilex aquifolium*, Mulgrave Woods, Yorks., C. Crossland, Sept. 08; Powers Court, Dublin, C. Crossland, Sept. 1898; Chislehurst, Kent, F. Currey, Nov. 1859.

*Nectria punicea* var. *ilicis* folder Herb. I.M.I.

On *Ilex aquifolium*, Solihull, Warwicks., E.W.M., April 22 (18363); Westcott, Surrey, E.W.M., Aug. 23 (18302); Penkridge, Staffs., N. C. Preston, April 38 (18365); Redemon, N. Ireland, E.W.M., Sept. 40 (34608); Haslemere, Surrey, E.W.M., Sept. 45 (1336); Mistly, Essex, M.B.E., May 48 (59650); Rufus Stone, Hants, A. H. S. Brown, Sept. 54 (57790); Forest of Dean, Glos., C.B., Sept. 55 (61045); Ranmore Common, Surrey, C.B., Jan. 56 (61774a); Dulverton, Somerset, C.B., May 57 (69424a & 69436); Leith Hill, Surrey, C.B., Oct. 57 (70788); Ashtead Common, Surrey, C.B., Feb. 58 (71878); Wootton, Surrey, C.B., Mar. 58 (72605); Gwydyr Forest, Llanrwst, C.B. & S.J.H., May 58 (73437) Type collection. *Ex. Herb. Ehrlich on Ilex aquifolium*, Westwick Woods, Norfolk, E.W.M., Oct. 34 (22834); Stratton Strawless Woods, Norfolk, E.W.M., Oct. 34 (22833); Westerham, Kent, E.W.M., April 35 (22837); Reigate, Surrey, E.W.M., April 35 (22835); Ashdown Forest, Sussex, E.W.M., April 35 (22836).

*Nectria punicea* var. *ilicis* collections in *Nectria punicea* folder in Herb. R.B.G. Kew

On *Ilex*, J. E. Vize, *Micro-fung.* Brit. 373; M. C. Cooke, Shere (ex. Herb. Cooke); C. Roumeguère, *Fung. Gall. Exs.* 2181; P. P. Strasser, *Krypt. Exs.* 1610; Prof. Balfour, Oxford, Feb. 1887; J. S. Gamble, Highfield Woods, Hants, Jan. 13.

*Nectria fuckeliana* spec. nov.

(*N. cucurbitula* in Fuckel's *Symb. Mycol.* p. 180, 1870; non *N. cucurbitula* (Tode ex Fr.) Fr.)

When Miss Dingley (1951) described *Nectria pinea* to replace *N. cucurbitula*, which she considered to be a nomen confusum, she did not appreciate the extent of the confusion that existed. In Europe, the modern concept of *N. cucurbitula* was based on Fuckel's *Fung. Rhen. Exs.* 983, but this was not the species to



which Fries had applied the name. He used it for what, until now, has commonly been called *Ophionectria cylindrospora*.

This species has long multiseptate ascospores which produce ascocidia in the ascus. It is further discussed under the name *Scolecconectria cucurbitula*.

There are also two species of *Nectria* on conifers which have hitherto been treated as one, under Fuckel's concept of *N. cucurbitula*. One is now distinguished as *N. pinea* Dingley and the other is based on Fuckel's Fung. Rhen. No. 983, issued as *N. cucurbitula*. As this latter name has already been used, the name *N. fuckeliana* is proposed for this species.

All three are confined to coniferous trees and the characters separating them are tabulated below:

	<i>Nectria fuckeliana</i> 'Coccineoid'	<i>Nectria pinea</i> 'Mammoid'	<i>S. cucurbitula</i> 'Aquifolioid'
Perithecia	In groups of 10-100 300-400 $\mu$ dia.	Scattered or in small groups, 400-500 $\mu$ dia.	Groups of 10-20, 250-400 $\mu$ dia.
Ascospores	13-16 $\times$ 5-6 $\mu$	16-22 $\times$ 7-10 $\mu$	36-55 $\times$ 2-3.5 $\mu$
Ascocidia	None	None	4-6 $\times$ 1-1.5 $\mu$
Microconidia	6-9 $\times$ 2.5-5 $\mu$	None	4-6 $\times$ 1 $\mu$
Macroconidia	3-septate only	4-5 septate	None
(when mature)	33-40 $\times$ 4-5 $\mu$	52-75 $\times$ 5-7 $\mu$	

*Nectria fuckeliana* spec. nov.

*Stromata* erumpentia appanata, 1-2 mm. diametro, 0.5-1 mm. lata parenchymatica.

*Perithecia* caespitosa, stroma omnino tegentia, ellipsoidea, levia, ostiolo minute papilliformi ornata, rubra vel fuscorubra, 300-400  $\mu$  diam.

*Asci* cylindracei, apice rotundati et cingulo refringenti porum circum ambienti praediti, octospori, 86-120  $\times$  10-12  $\mu$ .

*Ascospores* monostichae vel subdistichae, fusiformes, hyalinae, medio constrictae, 1-septatae, 13-16  $\times$  5-6  $\mu$ .

*In cultura*

*Mycelium* album, floccosum, ex hyphis hyalinis 3-4  $\mu$  crassis compositum.

*Microconidia* hyalina, ovalia vel cylindrica 6-9  $\times$  2.5-4  $\mu$  on pseudocapitulum aggregata.

*Macroconidiophora* ramosa; phialidibus subulatis terminala, 18-30  $\times$  2.5-3  $\mu$ .

*Macroconidia* Fusario similea, hyalina, curvula, fusiformia, 3-septata 33-40  $\times$  4-5  $\mu$ , in cumulo glutinosa.

*Habitat* in ramis pinorum, Fuckel, Fungi Rhen. No. 983 ut *Nectria cucurbitula* Fr., in Herb. R.B.G. Kew.

#### DESCRIPTION

Perithecia develop in groups of 10-100 on discrete stromata that arise in the phelloderm and rupture the overlying periderm of the host. Each stroma is 1-2 mm. in diameter and 0.5-1 mm. thick, and composed of homogeneous pseudoparenchymatous tissue formed of hexagonal thin-walled cells 10-20  $\mu$  in diameter. Occasionally the perithecia develop on bare wood and in this case the stroma exists merely as a cushion below the perithecia.

The smooth-walled, broadly ovate perithecia, with a short indistinct ostiolar papilla, are very regular and characteristic in appearance. When young they are bright red but become deep maroon when mature and measure  $300\text{--}400\ \mu$  in diameter. In section the lateral wall is  $60\text{--}80\ \mu$  wide and formed of three zones.

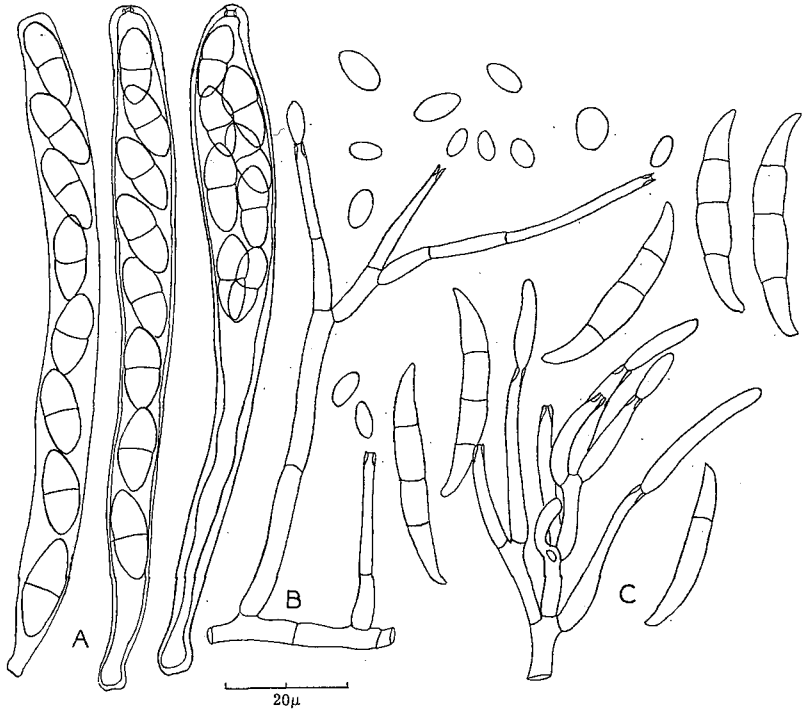


FIG. 16. *Nectria fockeliana*. A, asci and ascospores; B, microconidiophores and conidia; C, macroconidiophores and conidia.

The outer, which is  $36\text{--}40\ \mu$  wide, shows a close relationship to the 'mammoidea' group but here the cell structure is not so obscured as in most species in this group. These cells are elongated with the longest axis at right angles to the surface of the wall and measure  $12\text{--}16 \times 3\text{--}4\ \mu$ . The central zone is  $14\text{--}18\ \mu$  wide and formed of elongate cells with the longest axis parallel to the surface of the wall and cells  $8\text{--}14 \times 2\text{--}4\ \mu$ . The cavity of the perithecium is lined by several layers of very thin-walled cells which are crushed as the asci mature, and these cells form the inner third region.

Asci are cylindrical with a rounded apex possessing a well-marked ring. They have eight monostichous but later obliquely monostichous and then distichous ascospores. When monostichous the asci are  $86\text{--}120 \times 8\text{--}9\ \mu$ , but as the spores become distichous they widen apically to  $10\text{--}12\ \mu$ . Paraphyses are abundant and usually persist until the asci mature. Ascospores are broadly fusiform to ellipsoid and slightly constricted at the central septum, they are hyaline but may become light brown and slightly verrucose at maturity when they measure  $13\text{--}16 \times 5\text{--}6\ \mu$ .

## CULTURES

Ascospores isolated on to malt and on to potato dextrose agar grow readily and in 14 days the colony is 2–3 cm. long and the width of the test-tube. The hyphae forming this mycelium are full of oil drops; the colony is white, floccose, and produces masses of microconidia; the only discoloration of the media is a slight yellowing on potato dextrose agar.

All the isolations made of this species show a reluctance to form secondary conidia except when placed in direct sunlight even though they produce perithecia in indirect light in 6–8 weeks. The microconidiophores are formed laterally on hyphae 3–3.5  $\mu$  wide and may be simple, or branched once or twice. These branches terminate in subulate phialides 17–25  $\mu$  long and 1–1.5  $\mu$  at the base and terminating in an apical collar. Primary conidia are hyaline, oval, occasionally almost globose, and measure 6–9  $\times$  2.5–5  $\mu$ .

Macroconidia develop in 3–4 weeks but only in cultures in direct sunlight, where they form orange pustules over the surface of the colony. Secondary conidiophores are branched several times and each branch terminates in 1–4 phialides, these are subulate 18–30  $\mu$  long and 2.5–3  $\mu$  at the base.

Macroconidia are curved, *Fusarium*-like, broadest at the centre and narrowing apically to a point and basally to a *Fusarium*-like foot-cell, they are hyaline, 3-septate, and measure 33–40  $\times$  4–5  $\mu$ .

## SPECIMENS EXAMINED

*Nectria cucurbitula* folder Herb. R.B.G. Kew

Fuckel, Fung. Rhen. No. 983 *Nectria cucurbitula* (type); Herb. Barbey-Bois. No. 855, *N. cucurbitula* (ex Herb. Fuckel, Fung. Rhen. 983); Kunze, Fung. Select. Exs., No. 105 *N. cucurbitula*; Ludwig, Flora Westfalen, *N. cucurbitula*; Rabenhorst, Fung. Europe. No. 1235 *N. cucurbitula*; Rabenhorst, Fung. Europ. et ex. Europ. No. 4258 *N. cucurbitula*; Roumeguère, Fung. Gall. Exs. Nos. 1016 and 1292 *N. cucurbitula*; Sydow, Mycotheca germ. No. 323 *N. cucurbitula*; Sydow, Mycotheca March. No. 472 *N. cucurbitula*.

*Nectria fuckeliana* folder Herb. I.M.I.

On *Abies*, Vindobon, Krypt. Exs. No. 965. On *Larix*, Swallow Falls, Betws-y-coed, Wales, C.B., May 58 (73333). On *Picea*, Richmond, Nova Scotia, Canada, R. E. Balch, Aug. 31 (52082); Lund, Sweden, J.E., April 34 (52083); Bokeberg, Sweden, J.E., April 34 (52084 & 52085); Sachsenwald, Hamburg, Germany, J.E., April 34 (52088); Glentress Forest, Peebles, Scotland, M. Wilson & J.E., March 35 (22814); Benmore Estate, Argyllshire, Scotland, J.E. & C. G. C. Chesters, March 35 (52089); Braco, Perthshire, Scotland, J.E. and C. G. C. Chesters, March 35 (52094); Bin Forest, Aberdeenshire, Scotland, J. Walker, June 58 (73789); Loch Fyne, Argyll, J. S. Murray, July 58 (74201a). Exsiccata: A. Ludwig, Flora Westfalen (16975 & 22039); Flora Lothringer (16974).

*Nectria hederæ* spec. nov.

(The outstanding character of this species is the formation of the primary conidia in chains.)

*Stromata* parva vel vestigialia.

*Perithecia* ovata, rubra vel fusciorubra, 200–300  $\mu$  lata, 270–300  $\mu$  alta, apice applanata.

*Asci* cylindrici, basi truncati, apice rotundati et cingulo refringenti porum circum ambienti praediti, octospori 80–95  $\times$  7–9  $\mu$ .

*Ascospores* monostichae, obliquae, hyalinae vel pallide brunneae, ellipsoideae, 1-septatae, 12–15  $\times$  4.5–6  $\mu$ .

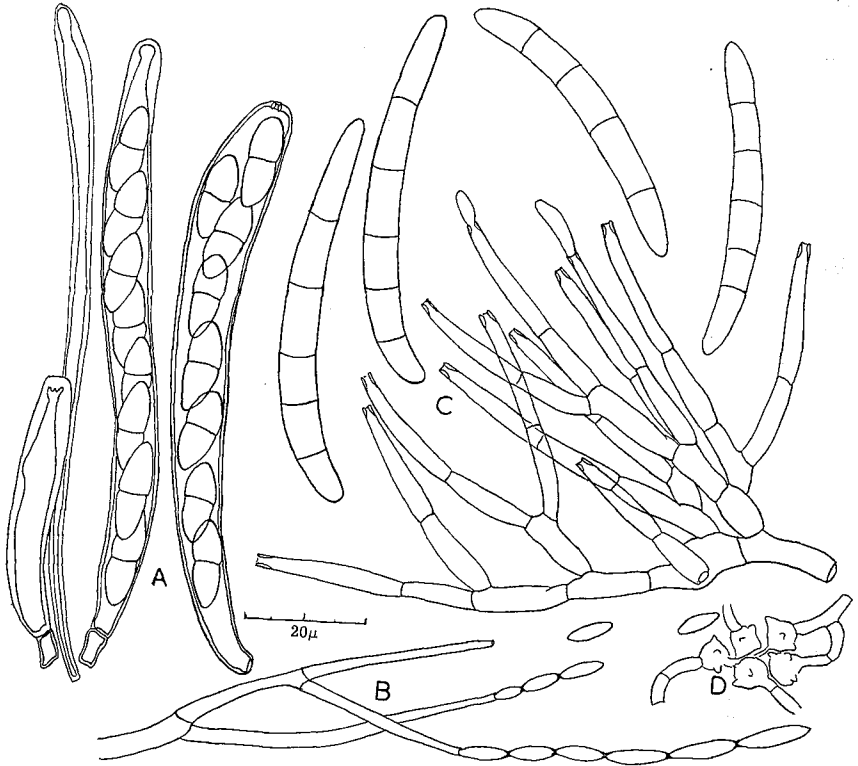


FIG. 17. *Nectria hederae*. A, asci and ascospores; B, microconidiophores and microconidia in chains; C, macroconidiophores and macroconidia; D, chlamydospores.

#### *In cultura*

*Mycelium* album ex hyphis sparsis hyalinis compositum.

*Microconidiophora* ramosa, prostrata vel erecta, phialidibus subulatis terminata, 24–30  $\times$  2–3  $\mu$ .

*Microconidia* in catenulas ad 400  $\mu$  longas producta hyalina, fusiformia 6–9  $\times$  2–3  $\mu$ .

*Macroconidiophora* ramosa, hyalina, phialidibus subulatis terminata, 22–36  $\times$  4–5  $\mu$ .

*Macroconidia* cylindrica, utrinque rotundata, curvula, 5-septata 52–78  $\times$  5–7  $\mu$ .

*Habitat* in ramis *Hederae helix*, Kew Gardens, Surrey, England; Typus I.M.I. 58770a.

The perithecia occur directly on the cut ends of stems or on the periderm of *Hedera helix*. They are ovate with a slightly flattened ostiolar disc, in the centre of which is a small papilla bearing the ostiole. Initially the perithecia are

bright red but gradually they become darker in colour, they measure 250–300 (200–300)  $\mu$  in diameter and 270–300  $\mu$  in height. Small hyaline 'bristles' occasionally seen on the walls are the primary conidiophores, these will produce phialides and primary conidia in chains if the perithecia are placed in a damp chamber when fresh.

In section, the lateral wall of the perithecium is 25–35  $\mu$  wide and has three indistinct regions; the outer is 16–20  $\mu$ , has thick-walled cells 6–10  $\times$  4–5  $\mu$ . The central region is formed of three to four layers of elongated cells 10–16  $\times$  2–3  $\mu$  with thinner walls than those of the cells in the outer region. Apically the cells of this region form the disc. The inner region is formed of several layers of very thin-walled elongate cells which are crushed as the perithecium matures.

The asci are cylindrical, shortly truncate and with a rounded or flattened apex containing a pore, they measure 80–95  $\times$  7–9  $\mu$ .

The ascospores are obliquely monostichous, hyaline, elliptical to navicular, 12–15  $\times$  4.5–6  $\mu$ . When fully mature and just before discharge they may become distichous, light brown, verrucose, and slightly constricted at the central septum.

#### CULTURAL CHARACTERS

Ascospores germinate readily to produce hyphae from one or both cells of the spore and these form a sparse hyaline mycelium on the surface of the agar in test-tubes in 4–6 days. After this time microconidia of the form genus *Paecilomyces* begin to develop. The branched conidiophores form from adjacent cells of the superficial hyphae and the branches terminate in subulate phialides 24–30  $\times$  2–3  $\mu$ . Conidia formed in chains from these phialides are hyaline fusiform and rather flattened at the ends, they measure 6–9  $\times$  2–3  $\mu$ . Macroconidiophores may develop a little later and on the same mycelium, these are more branched than the primary ones and terminate in phialides 22–36  $\times$  4–5  $\mu$ . Macroconidia are *Cylindrocarpon*-like with rounded ends, generally 5-septate at maturity and measure 62–66  $\times$  6 (52–78  $\times$  5–7)  $\mu$ . In 5–8 weeks on corn meal, potato dextrose, and malt agar, hyphae 5–7  $\mu$  wide with cells 25–30  $\mu$  long develop, these become light brown and form discrete stromata on the surface of the agar. These stromata become covered with lageniform phialides 14–20  $\times$  3–4  $\mu$  which produce abundant macroconidia; these are very conspicuous in older cultures as they adhere together in cream-coloured cones.

Chlamydospores also form sparsely in older cultures, they are 5–6  $\mu$  in diameter and have several short lateral spines. No perithecia developed in my agar cultures; sub-cultures on autoclaved elm twigs in flasks formed cones of secondary conidia in 4–5 weeks and these were followed by perithecia which were dispersed over the surface of the twigs.

No pronounced discoloration of the media occurred in the agar cultures.

#### SPECIMENS EXAMINED

*Nectria hederæ* folder Herb. I.M.I.

On *Hedera helix*, Kew Gardens, Surrey, C.B., Dec. 54 (type coll. 58770a); Jan. 55 (59405).

## NECTRIA MAMMOIDEA GROUP

This section includes *Nectria* species with perithecia 350–700  $\mu$  in diameter and with a darker ostiole than venter, giving a two-tone coloration to the perithecium; early in development they are orange-yellow and gradually become deep reddish brown to almost black. They are globose with a flat or slightly convex apical disc and occur in groups of 3 to 6 on a mixed stroma that forms in the cortex and finally becomes weakly erumpent. The wall has typically three regions, the outer having two to three layers of thin-walled globose cells as in *N. mammoidea* var. *rugulosa*, this may be reduced to a single layer as in *N. pinea* or be entirely absent as in *N. mammoidea* var. *rubi*. The most characteristic part of the wall is the central region referred to as the pseudopalisade; this occupies half to two-thirds the width of the wall. It is formed of convoluted hyphae densely compacted and with the longest axis of the cells at right angles to the surface of the wall. The cells are laterally joined by anastomosis and agglutination. The inner wall is composed of two regions that are not clearly separable; below the pseudopalisade zone are several layers of globose or slightly elongate thick-walled cells and these merge into layers of very thin-walled elongate cells that line the ascus cavity. The apical disc is formed by the globose cells just below the pseudopalisade region. The pseudopalisade region is not present in the basal part of the wall, being replaced by thick-walled globose cells similar to those forming the ostiolar disc.

Asci are typically cylindrical with an apical ring and eight monostichous to apically distichous ascospores.

Ascospores are broadly fusoid with a single central septum and are hyaline to pale yellow in colour.

Macroconidia develop on the perithecial stroma or directly on the host as cream-coloured pustules or cones. Sterile brown hyphae occur between the perithecia on the host.

## CULTURAL CHARACTERS

Primary conidia are absent in culture and secondary conidia are referred to the genus *Fusarium* (Pethybridge, 1927) or *Cylindrocarpon*. Perithecia often develop in older cultures where the agar is usually dark purple in colour. Chlamydospores are also formed in the older cultures.

## KEY TO SPECIES

Outer perithecial wall warted . . . . .	<i>N. veuillotiana</i>
Outer perithecial wall roughened, powdery . . . . .	<i>N. mammoidea</i> var. <i>rugulosa</i>
Outer perithecial wall finely roughened . . . . .	<i>N. mammoidea</i> (in part)
Outer perithecial wall smooth, shining . . . . .	1
1. Ascospores 12–14 $\times$ 5–6 $\mu$ . . . . .	<i>N. mammoidea</i> var. <i>rubi</i>
1. Ascospores 15–18 $\times$ 6–7 $\mu$ . . . . .	<i>N. mammoidea</i> (in part)
1. Ascospores 16–22 $\times$ 7–10 $\mu$ . . . . .	<i>N. pinea</i>

*Nectria mammoidea* Phil. & Plowr., *Grevillea*, iii, p. 126, 1875.

*Nectria discophora* Fuckel (Non Mont. teste Höhn. & Weese, *Ann. mycol. Berl.*, viii, p. 465, 1910) Fung. Rhen. Exs. No. 1581, 1865.

*Nectria nelumbicola* P. Henn., *Verh. bot. Ver. Brandenburg*, xl, p. 151, 1898. Teste Höhn. & Weese, *Ann. mycol. Berl.*, viii, p. 467, 1910.

*Creonectria mammoidea* (Phil. & Plowr.) Seaver, *Mycologia*, 1, p. 188, 1909.

*Cylindrocarpon ianthothele* Wollenw. var. *majus* Wollenw. *Z. Parasitenk.*, 1, p. 161, 1928.

## DESCRIPTION

The perithecia occur on the periderm or epidermis of many deciduous trees and herbaceous plants. The species was first cultured from ascospores obtained from the perithecia on seeds of *Smyrniun olusatrum* and it has since been grown from ascospores from perithecia on the bark of six deciduous trees.

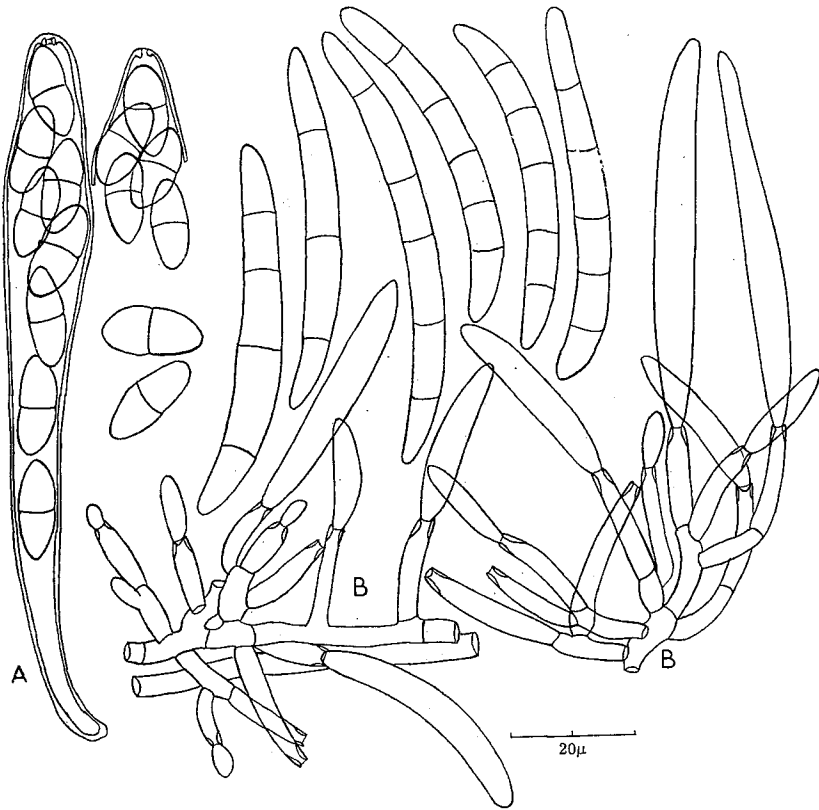


FIG. 18. *Nectria mammoidea*. A, asci and ascospores; B, conidiophores and conidia.

The perithecia are solitary to gregarious and usually on a loose pseudostroma, formed in the periderm, of hyphae, pseudoparenchyma, and host tissue. When they form on bare wood this stroma is usually absent. Brown sterile hyphae are usually present between the perithecia.

The subglobose perithecia have a prominent convex apical disc and measure

400–700  $\mu$  in diameter. The outer wall may be smooth, shining or slightly verrucose,<sup>1</sup> and the colour changes during development from orange to deep reddish brown with the apex becoming almost black.

In section the lateral wall is 45–70  $\mu$  thick and has 3–4 regions. The outer, which may be absent, consists of globose cells 10–14  $\mu$  in diameter forming 1–2 layers. Below this is the typical pseudopalisade layer of this group, 28–40  $\mu$  wide. The third region below the palisade is formed of 2–3 layers of elongate thick-walled cells which apically form the disc. The inner layer is composed of elongate thin-walled cells and these give rise basally to the paraphyses and laterally to the periphyses. In the basal region the pseudopalisade layer is replaced by cells 10–12  $\times$  3–4  $\mu$  with thick walls.

The asci are cylindrical to clavate and rounded at the apex which contains a central chitinoid pore; they have 6–8 obliquely monostichous or obliquely distichous ascospores and measure 90–130  $\times$  8–10  $\mu$ .

Ascospores are hyaline, smooth walled, ellipsoid to broadly fusoid; they may become light brown and slightly constricted at the central septum at maturity when they measure 16–17  $\times$  6.5–7 (14–20  $\times$  6–8)  $\mu$ .

#### CULTURES

Single ascospores isolated on to potato dextrose and on to malt agar form a colony 2–3 cm. long in 14 days. On malt agar the aerial mycelium forms zonate rings and a strong purple discoloration of the agar occurs at about the same time as conidia begin to develop, i.e. in 8–10 days. The zones of formation have a slimy appearance and this soon covers the whole surface of the colony. In the aerial mycelium the coloration is due to drops of purple-coloured liquid secreted from the hyphae. On potato dextrose agar growth is more erumpent, floccose, and the discoloration is more brown.

Conidiophores arise as short lateral branches to the hyphae. Typically each consists of a stalk cell with 4–8 branches and each branch carries 2–4 terminal phialides. These phialides are hyaline, doliform, 15–24  $\times$  3–6  $\mu$  and have a thickening of the lateral wall apically to form a collar.

Conidia are cylindrical, slightly curved with rounded ends, and generally narrower towards the base. When mature they are 3–7 septate and measure 54–72  $\times$  6–7  $\mu$ .

Perithecia form in abundance on both potato dextrose and malt agar in about 3 weeks but only in the first isolates, successive subcultures show a rapid decline in perithecial formation.

#### SPECIMENS EXAMINED

##### Type material

*Nectria mammoidea* Ph. & Pl., on dead stems of *Ulex europaeus*, North Wootton, Jan. 1874. Leg. C. B. P. Parts of this collection are in Herb. R.B.G.

<sup>1</sup> The verrucose appearance of the perithecial wall is due to the outer globose cells mentioned in the description of the wall structure. It should not be confused with the large globose cells present in *Nectria mammoidea* var. *rugulosa*. This variety is also culturally distinct; cultures from the verrucose perithecia of a collection of *N. mammoidea* are identical with cultures from the smooth-walled perithecia.



Kew, Edinburgh, and in the British Museum. Although the material in Kew is now poor, that in the other two herbaria is in fair condition.

*Nectria mammoidea* folder Herb. I.M.I.

(One collection only is cited for each host.)

On *Acer*, Cleve Coombe, Bristol, A. H. S. Brown, Sept. 55 (61054b). On *Brassica*, Beverley, Yorks., J.W., Mar. 53 (57454). On *Fagus*, Gwydyr Forest, Llanrwst, Wales, C.B., May 58 (73334a). On *Populus*, Wetherby, Yorks., C.B., April 58 (72790). On *Quercus*, Swindon Park, Yorks., S.J.H., Oct. 47 (19262). On *Smyrniium*, Surlingham, Norfolk, E.A.E., May 57 (69361). On *Ulmus*, Wetherby, Yorks., C.B., April 58 (72789a). Five collections from Britain and one from New Zealand are present on undetermined hosts.

*Nectria mammoidea* Phil. & Plow. var. *rubi* (Osterw.) Weese, *Zeitsch. Garungsphysiol.*, 1, p. 129, 1912.

*Nectria rubi* Osterw., *Ber. dtsh. bot. Ges.*, xxix, pp. 611-622, 1911.

*Hypomyces rubi* (Osterw.) Wollenw., *Phytopath.*, iii, pp. 224-225, 1913.

*Cylindrocarpon ianthothele* Wollenw., *Ann. mycol. Berl.*, xv, p. 56, 1917.

This variety is associated with the roots of raspberry canes and is usually found after these have begun to show signs of disease. There is, however, some doubt as to the actual causal organism as most of the experimental evidence using *Nectria mammoidea* var. *rubi* appears to be negative. Wollenweber (1926) stated that it was pathogenic but later in a letter to Pethybridge he stated that this had not been proved.

Its occurrence in the British Isles was first described by Pethybridge and Lafferty (1916) from Ireland. Miss Alcock recorded it from Scotland (1927) and both Pethybridge and Natrass (1927) gave extensive descriptions of the fungus and discussed its occurrence in England.

No fresh material has been collected or received by the writer and the description is based on collections and cultures by Miss Alcock, Osterwalder's culture now at the Centraalbureau f. Schimmelcultures and material collected by Pethybridge, Natrass, and Harris.

#### DESCRIPTION

Perithecia occur below the soil surface, most frequently around the transition region between root and cane. They are ovoid to globose, smooth-walled, light orange-red but becoming dark reddish brown to almost black, and measure 350-550  $\mu$  in diameter.

In section the lateral wall is 60-70  $\mu$  wide and formed of 3 regions; the inner region consists of only 1-2 layers of elongate thin-walled cells. The central region is formed of very thick-walled cells 10-14  $\times$  2-4  $\mu$ , and the outer is the pseudopalisade region and is 40-46  $\mu$  thick.

The asci are cylindrical and rounded at the apex which bears a collar. They measure 90-110  $\times$  7-9  $\mu$  and have eight obliquely monostichous and occasionally distichous ascospores.

The ascospores are hyaline, elliptical, slightly constricted at the central septum and measure 12-14  $\times$  5-6.5  $\mu$ , when mature they are light brown and faintly rugulose.

## CULTURES

Dried cultures in Herb. I.M.I. show purple discoloration of the agar with bay-brown aerial mycelium. Conidiophores arise laterally in tufts from mycelial ropes, they are dichotomously branched and each branch terminates in one or more doliform phialides.

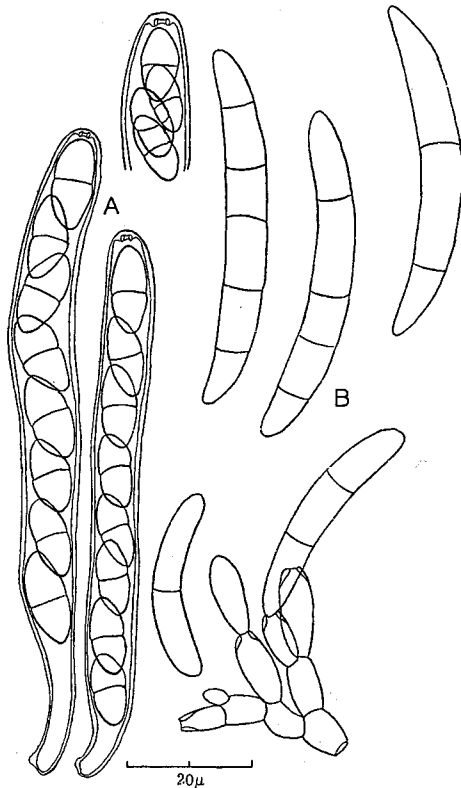


FIG. 19. *Nectria mammoidea* var. *rubi*. A, asci and ascospores; B, conidia and conidiophores.

Macroconidia only are present; these are hyaline cylindrical and slightly curved with rounded ends, although basally a *Fusarium*-type foot cell may be formed. They have 3-5 transverse septa and measure  $45-60 \times 6-8 \mu$ .

Pethybridge (1927) stated that the 'heel' is usually absent on conidia formed in rapidly growing cultures.

## SPECIMENS EXAMINED

*Nectria mammoidea* var. *rubi* folder Herb. I.M.I.

On *Rubus idaeus*, from Ireland, G. H. Pethybridge, no date (52179); Aberdeen, Scotland, N. L. Alcock, 1925 (52178); Long Ashton, Bristol, R. M. Nattrass, 25 (52180); Beaulieu, Inverness-shire, N. A. Alcock, July 27 (52182); Merstham, Surrey, R. V. Harris, Aug. 28 (22841); Nelson, Tapawere, N.Z., P. Fry, Jan. 49 (50403); J. Dingley, 56 (70017). Switzerland, Osterwalder, from C. B. S (52934).

*Nectria mammoidea* var. *rugulosa* Weese, *S.B. Akad. Wiss. Wien*, 1, cxxv, p. 552, 1916.

## DESCRIPTION

Perithecia gregarious on the bark or wood of deciduous trees, they are 550–700  $\mu$  in diameter with a flattened ostiolar disc 130–200  $\mu$  in diameter. In the early stages of development they are yellow with a red apical disc but gradually

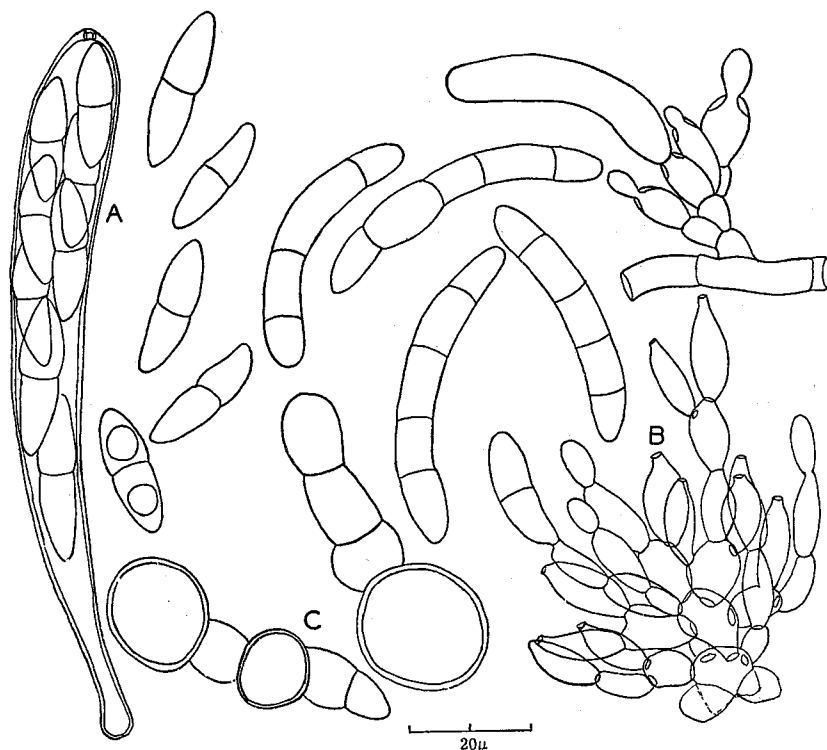


FIG. 20. *Nectria mammoidea* var. *rugulosa*. A, ascus and ascospores; B, conidia and conidiophores; C, chlamydospores.

they become reddish yellow with a light reddish-brown apical disc and finally reddish brown with the apical disc almost black. In section the wall has three regions; the outer of these has two to three layers of thin-walled hyaline and irregularly globose cells 12–22  $\mu$  in diameter. The middle layer 24–30  $\mu$  thick is the characteristic 'mammoidea' pseudopalisade layer. The inner layer 16–24  $\mu$  thick is formed of 5–8 layers of hyaline fusoid cells 30–60  $\times$  3–4  $\mu$ . Their shape is due to compression and is more marked in the inner layers where the cells have thinner walls.

The asci are cylindrical to clavate, 100–135  $\times$  11–13  $\mu$  with an apical pore and eight obliquely monostichous, but later apically distichous, ascospores.

The ascospores are hyaline, smooth, elliptical to broadly fusoid with a slight constriction at the single central septum, they measure 18–21  $\times$  6–7 (17–35  $\times$  6–8)  $\mu$ .

No conidia were found on the host, although from the occasional presence of an effete and disintegrating conidiophore stroma it is presumed that conidial development preceded perithecial formation.

#### CULTURES

Ascospores were isolated on to malt and potato dextrose agar. Growth on potato dextrose agar was more rapid than on the malt and the aerial mycelium became more dense. After 14 days the media had become darker and the surface was covered with a floccose mycelium formed of narrow hyaline hyphae  $2-3\mu$  wide with cells  $12-18\mu$  long. In older cultures these narrow hyphae were almost replaced by thick dark brown hyphae with cells  $18-26 \times 4-9\mu$  and these tend to aggregate together to form ropes.

Macroconidia are first formed from phialides which arise terminally on short lateral branches on the broad hyphae. These conidiophores are characteristic of the species in having short broad cells which branch once or twice and terminate in ovate to obovate phialides  $9-12 \times 6-7.5\mu$ . Later macroconidia are formed on discrete pustulate stromata, these stromata are formed from an aggregation of globose cells which give rise to numerous branches, these may form further branches apically and 2-3 cells long, each of which terminate in an obpyriform phialide  $10-12 \times 5-6\mu$ .

The conidia are hyaline, cylindrical, with rounded ends and usually slightly curved. When mature they are 4-septate and measure  $45-55 \times 6-7\mu$ . As the cultures dry out the cells of the conidia often form chlamydospores; these are thick walled, globose, pale brown in colour, and measure  $18-20\mu$  in diameter.

#### SPECIMENS EXAMINED

*Nectria mammoidea* var. *rugulosa* folder Herb. I.M.I.

On *Acer*, Bolton Abbey, Yorks., W.G.B., April 56 (62739). On *Quercus*, Hardcastle Craggs, Yorks., R. Watling, April 57 (69124).

*Nectria veuillotiana* Roum. & Sacc., *Rev. Mycol.*, ii, p. 189, 1880.

*Sphaerostilbe sanguinea* Fuckel, *Symb. Myc.*, Nachtr. iii, p. 22, 1877 (non *N. sanguinea* Bolt. ex. Fr.).

*Atractium candiduli* Sacc., *Syll. Fung.*, ii, p. 512, 1883; sub. *Sphaerostilbe sanguinea* Fuckel.

*Dialonectria veuillotiana* (Sacc. & Roum.) Cooke, *Grevillea*, xii, p. 110, 1884.

*Cylindrocarpon candidulum* (Sacc.) Wollenw., *Z. Parasitenk.*, 1, p. 160, 1928.

#### DESCRIPTION

Perithecia occasionally solitary but mostly in groups seated on an erumpent stroma. The latter is pseudoparenchymatous, yellow in colour with thin-walled cells  $14-18 \times 10-14\mu$ . Perithecia, which usually form in succession on the surface of this stroma, are globose with an apical disc which bears the ostiole on a small central papilla. They have a warted outer wall which is yellow becoming bright red and finally brown in colour, the ostiolar disc is smooth and slightly darker

than the rest of the perithecium; they measure  $300-500\ \mu$  in diameter. In section the lateral wall is formed of three regions and is  $50-80\ \mu$  wide. The outer, which varies in relationship to the position and stage of development of the warts, is composed of strongly pigmented, thick-walled globose cells  $12-20 \times 10-18\ \mu$ . The central region is  $20-30\ \mu$  wide, the cells for the most part are elongated to globose  $16-25 \times 7-12\ \mu$  but at maturity, especially in the upper part, the wall

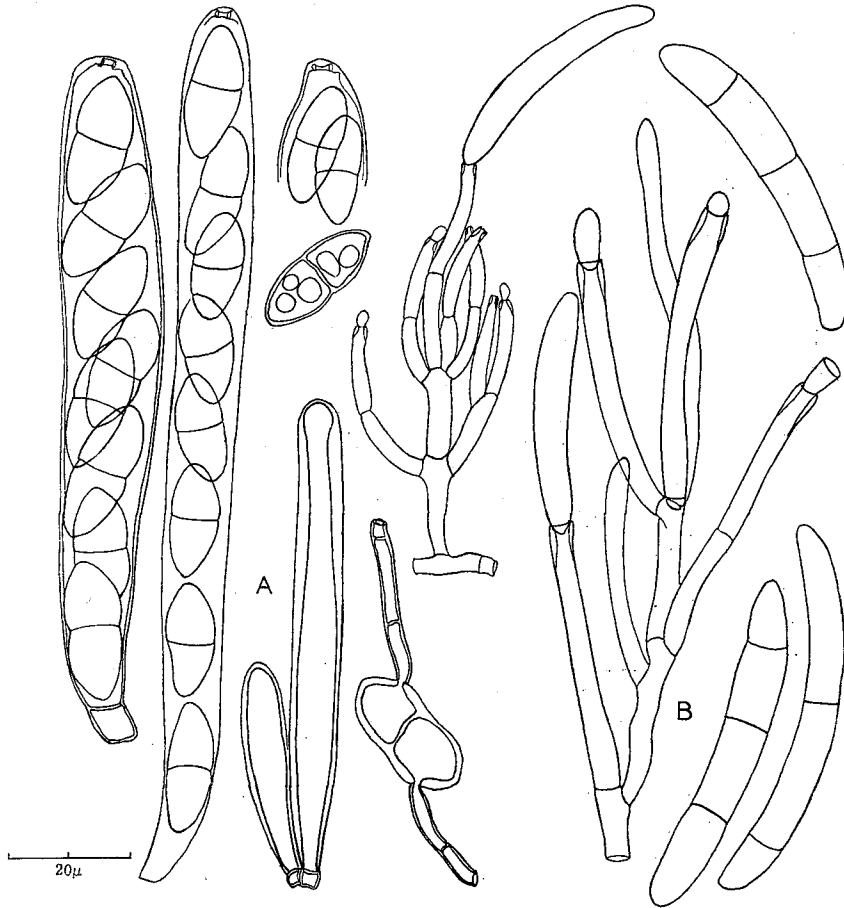


FIG. 21. *Nectria veuillotiana*. A, asci and ascospores; B, conidia and conidiophores.

assumes by convolution and radial elongation of the cells the characteristic pseudopalisade tissue of the *Mammoidea* group. The third region lining the perithecial cavity is formed of very thin-walled cells which tend to collapse at maturity, these cells measure  $20-30 \times 3-4\ \mu$ .

The asci are cylindrical with a flattened apex bearing a well-marked ring and measure  $108-130 \times 9-12\ \mu$ . The eight obliquely monostichous ascospores may become distichous at maturity; they are hyaline ellipsoid, slightly constricted at the central septum, and measure  $17-22 \times 7-9\ \mu$ .

## CULTURES

Ascospores isolated on to malt and potato dextrose agar in test-tubes produced a colony 3 cm. long in 4 weeks. From below this is reddish brown to purple in the centre and lighter towards the edge. From above it is sparse, white and floccose, with a central area of approximately 10 mm. in diameter of densely branched hyphae formed predominately of two types. The first is thin walled, sparsely septate, and  $1-1.5\ \mu$  in diameter. The second type is  $1.5-3\ \mu$  in diameter with cells  $24-40 \times 3-3.5\ \mu$ . These distinct hyphae show frequent anastomosis. The phialides arise in this central region from lateral branches of the thicker mycelium each of which produces several phialides. These are  $22-28 \times 3-4\ \mu$ , almost cylindrical and with a thickening of the lateral wall near the apex to form a collar.

The macroconidia develop as a growth of the inner wall of the phialide through the terminal pore, and this begins as a small swelling of the thin wall covering the apex of the phialide. Gradually this elongates and forms a cylindrical spore, usually slightly curved, and with smooth rounded ends, measuring:

aseptate	$30-55 \times 5-8\ \mu$
3-4 septate	$46-57 \times 5-7\ \mu$
4-7 septate	$50-60 \times 5-7\ \mu$

Macroconidia are only produced in this restricted central pseudostromatic region where they form white cones. No microconidia were found.

## SPECIMENS EXAMINED

*Nectria veuillotiana* folder Herb. R.B.G. Kew

Roumeg. Fung. Gall. Exs. 1076 *Nectria veuillotiana* (collection authentic for name).

*Sphaerostilbe sanguinea* folder Herb. R.B.G. Kew

Fuckel's, Fungi Rhen. Exs. 2655 *Sphaerostilbe sanguinea* nov. sp.

*Nectria peziza* folder Herb. B.M. Nat. Hist.

*Nectria peziza* Fr., Ralf. No. 557 ex Herb. Broome.

*Nectria veuillotiana* folder Herb. I.M.I.

On *Fagus*, Sevenoaks, Kent, J.E., Oct. 33 (22850); Burnham Beeches, Bucks., A. H. S. Brown, Oct. 55 (61280). On *Populus*, Benmore Estate, Argyll, J.E., and C. G. C. Chesters, Mar. 35 (22849). On *Salix*, Bann Meadows, Portadown, Armagh, C. M. Leach, Feb. 50 (39893).

*Nectria pinea* Dingley, *Trans. roy. Soc. N.Z.*, lxxix, p. 198, 1951.

An account of the confusion existing between *Nectria fuckeliana*, *Scoleconectria cucurbitula* and this species is given under *N. fuckeliana*, p. 56.

## DESCRIPTION

The perithecia are dispersed solitarily or in small groups on a weakly developed pseudoparenchymatous stroma which is barely erumpent through the periderm. Conidial formation precedes or accompanies perithecial development and forms

cream-coloured cones of macroconidia on the stroma. Erect, brown, sterile hairs, 2-4 septate and swollen towards the apex, and measuring  $200-350 \times 6-10 \mu$  are often present between the perithecia.

The perithecia are globose with a conical ostiolar disc, smooth to slightly rough-walled and orange-yellow becoming darker reddish brown, and measure

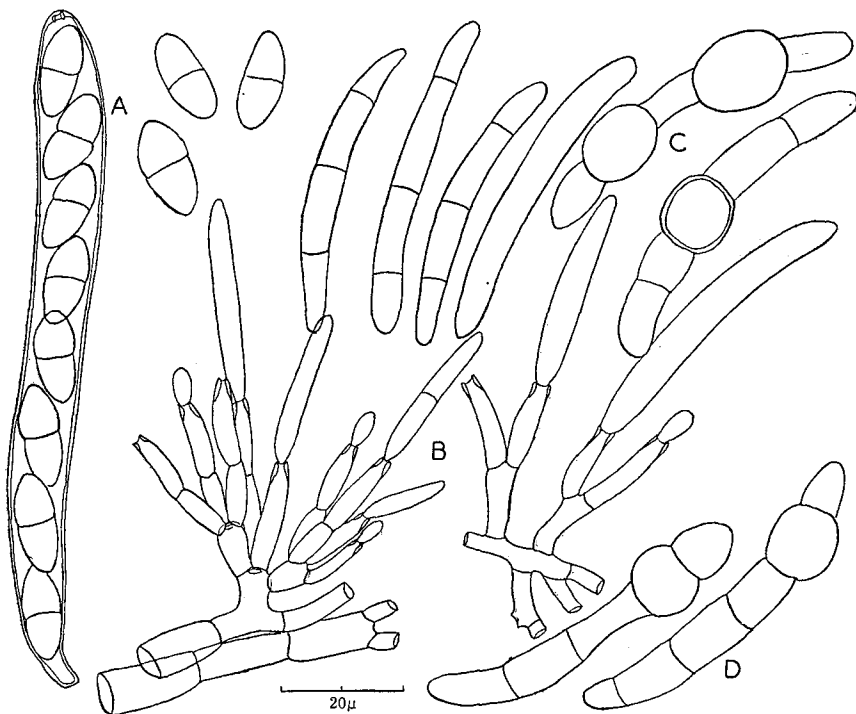


FIG. 22. *Nectria pinea*. A, ascus and ascospores; B, conidiophores and conidia; C-D, chlamydospores; D, from authentically named culture.

$400-500 \mu$  in diameter. In section the lateral wall is  $40-55 \mu$  thick with four regions. The outer is composed of one, occasionally two, rows of globose or slightly flattened cells  $8-14 \times 4-7 \mu$ . The next region is the pseudopalisade  $30-38 \mu$  thick. Below this are two to three layers of thick-walled cells  $8-10 \times 4-6 \mu$ . These cells merge into the inner layer of thin-walled elongate cells  $20-30 \times 3-4 \mu$  which line the perithecial cavity. Basally the pseudopalisade region is replaced by globose or somewhat flattened cells,  $8-12 \times 7-9 \mu$ .

The asci are cylindrical with a flattened apex bearing a ring, they measure  $80-110 \times 8-11 \mu$  and have eight monostichous to obliquely monostichous ascospores.

The ascospores are broadly fusoid, light brown when mature, and measure  $16-22 \times 7-10 \mu$ . Inter-ascial tissue may persist in the mature perithecium.

#### CULTURES

In the young colonies the first-formed hyphae are  $2-3 \mu$  wide and these form a colony 4-5 mm. in diameter in 7-14 days. About this time darker and thicker hyphae begin to form. These are  $6-7 \mu$  wide with cells  $60-70 \mu$  long and their

formation is usually accompanied by a purple to purple-brown discoloration of the agar. No microconidia have been found but macroconidia develop on laterally-formed conidiophores in 7-10 days. These conidiophores are shortly penicillate with the branches terminating in phialides 12-17  $\mu$  long and 4-5  $\mu$  broad. In older cultures the conidiophores tend to form only on discrete stromata.

Macroconidia 21 days on malt agar:

1-septate	30 $\times$ 3 $\mu$
2-3 septate	47-60 $\times$ 4-5 $\mu$
4-5 septate	52-75 $\times$ 5-7 $\mu$

Chlamydospores form in the cells of the macroconidia in older cultures, they are globose, thick walled, 10-12  $\mu$  in diameter. Perithecia usually form in 4-6-week-old cultures.

#### SPECIMENS EXAMINED

*Nectria pinea* folder Herb. I.M.I.

On *Abies*, Benmore Estate, Argyllshire, Scotland, J.E. & C. G. C. Chesters, Mar. 35 (52090). On *Larix* or *Picea*, Benmore Estate, Argyllshire, J.E. & C. G. C. Chesters, Mar. 35 (22816 & 52093); Hackness, Yorks., C. J. P. La Touche, April 55 (59904). On *Pinus*, Newport, Oregon, U.S.A., N. L. Gooding, Mar. 29 (52095); Benmore Estate, Argyllshire, Scotland, J.E. & C. G. C. Chesters, Mar. 35 (22815); Whakarewarewa, Rotorua, N.Z., J. B. Rawlings, Sept. 49 (50395) authentic for name; Rotorua, Auckland, J. Gilmour, Oct. 53 (70010); Cloughton Woods, Yorks., J.W., April 55 (59891); Thorntondale, Yorks., W.G.B., May 55 (62653). On *Pseudotsuga*, Benmore Estate, Argyllshire, Scotland, J.E. and C. G. C. Chesters, Mar. 35 (52091 & 52092).

#### THE EPISPHAERIA GROUP

The members of this group represent the true *Dialonectrias*, a genus proposed by Cooke for superficial separate perithecia without a stroma or subiculum. They are generally associated with effete Sphaeriaceous fungi and appear translucent when fresh. On drying they undergo a pinched lateral collapse. In culture they are slow growing and form *Fusarium* macroconidia of the *Eupionnotes* and *Macroconia* groups.

All these generalized characteristics have exceptions. In longitudinal sections the perithecia are often found to be seated on a thin stroma or byssus. *Nectria rishbethii*, *N. desmazierii*, and *N. brassicae* are not normally found in association with Sphaeriaceous fungi, and *Fusarium* macroconidia do not occur in the life history of *N. viridescens* and *N. rishbethii*.

The perithecia are generally small, 100-250  $\mu$  in diameter. Within the group are two types of wall development. The first is represented by *Nectria episphaeria*, *N. flavo-viridis*, *N. leptosphaeriae*, *N. desmazierii*, and *N. brassicae*. In these species the wall is not differentiated into regions except the 2-3 layers of very thin-walled cells lining the inner wall. The rest of the wall is formed of comparatively large oblong cells, the thick walls of the cells in the outer 1-2 layers become progressively thinner towards the inner layers. When the perithecia



undergo lateral collapse on drying, the apical papilla usually folds to form a crest on the top of the pinched perithecium.

The second section contains *Nectria magnusiana*, *N. rishbethii*, *N. purtonii*, and *N. viridescens*. These species have a thick wall formed of two regions. The outer consists of thick-walled globose cells and the inner of elongated thin-walled cells. The thick wall gives this species a wide ostiolar disc which is a further character of this section. If they collapse on drying the apical disc is not involved and the collapse or invagination is confined to the venter.

In all species the asci are cylindrical to clavate with an apical ring, although this is reduced to a pore in *Nectria magnusiana* and *N. desmazierii*.

The ascospores are broadly fusoid and generally become light brown when mature.

## KEY TO SPECIES

- A. Perithecial wall narrow 18–30  $\mu$ , not divided into 2-regions, individual cells easily discernible, if collapsed then apical disc is involved (folded or invaginated)
- Perithecia formed on the leaf scars or bark of *Buxus* . . . . . *N. desmazierii*  
 Perithecia formed on herbaceous stems, bright red . . . . . *N. brassicae*  
 Perithecia on or associated with Sphaeriaceous fungi:
- Ascospores 7–11  $\times$  3.5–5  $\mu$  . . . . . *N. episphaeria*  
 Ascospores 12–16  $\times$  6–8  $\mu$  . . . . . *N. flavo-viridis*  
 Ascospores 18–26  $\times$  6–8  $\mu$  . . . . . *N. leptosphaeriae*
- B. Perithecial wall wide, 26–55  $\mu$ , separable into 2-regions; outer cells thick walled, small, indistinct; if collapsed then apical disc, not involved (retains its shape)
- Perithecia developing on wood . . . . . *N. rishbethii*  
 Perithecia associated with Sphaeriaceous fungi:
- On *Diatrypella* . . . . . *N. magnusiana*  
 Associated with other pyrenomycetes:
- Perithecia appear gelatinous . . . . . *N. purtonii*  
 Perithecia red, opaque when dry . . . . . *N. viridescens*

## KEY TO CULTURES

(This key must be provisional as *Nectria brassicae* and *N. magnusiana* have not been grown, the conidial size is taken from the *Fusarium* associated with the perithecia on the host.)

1. Macroconidia fusiform (*Fusarium*-like) . . . . . 2  
 1. Macroconidia globose . . . . . 5
2. Cultures on malt or potato dextrose agar become green at, or before, macroconidial formation . . . . . *N. flavo-viridis*
2. Cultures colourless, salmon or orange-coloured . . . . . 3
3. Macroconidia markedly septate . . . . . 4
3. Macroconidia indistinctly septate
- a. 4.5–6  $\times$  1.5–2  $\mu$  . . . . . *N. magnusiana*  
 b. 20–24  $\times$  2  $\mu$  . . . . . *N. purtonii*  
 c. 35–50  $\times$  2.5–4  $\mu$  . . . . . *N. episphaeria*
4. Macroconidia acutely pointed and drawn out at the apex, 40–45  $\times$  4  $\mu$  . . . . . *N. brassicae*
4. Macroconidia with obtuse apex
- a. 45–60  $\times$  3–5  $\mu$  . . . . . *N. desmazierii*  
 b. 60–90  $\times$  6–8  $\mu$  . . . . . *N. leptosphaeriae*
5. Macro or secondary conidia globose
- a. Cultures deep green on potato dextrose agar . . . . . *N. viridescens*  
 b. Cultures brown on potato dextrose agar . . . . . *N. rishbethii*

*Nectria episphaeria* (Tode ex Fr.) Fr., Sum. Veg. Scand., ii, p. 388, 1849.

*Sphaeria episphaeria* Tode, Fung. Meckl., ii, p. 21, 1791.

*Sphaeria episphaeria* Tode ex Fr., Syst. Myc., ii, p. 454, 1823.

*Nectria viticola* Berk. & Curt., *Grevillea*, iv, p. 45, 1875.

*Dialonectria viticola* (Berk. & Curt.) Cooke, *Grevillea*, xii, p. 82, 1884.

*Dialonectria episphaeria* (Bolt. ex Fr.) Cooke, *Grevillea*, xii, p. 110, 1884.

*Fusarium aquaeductuum* Lagerh. var. *medium* Wollenw., *Z. Parasitenk.*, iii, pp. 298-299, 1931.

This species is the commonest of this group of *Nectrias* in Britain. The name which has been most frequently used for it, and hence under which it has been most frequently disposed in our herbaria, is *Nectria sanguinea*.

Many mycologists have considered *Nectria episphaeria* and *N. sanguinea* to be synonymous and have therefore used *N. sanguinea* because it is the earlier name. Fries (1823), Saccardo (1883), Winter (1887), and Seaver (1909) have treated them as distinct and used *N. episphaeria* for perithecia developing on Sphaeriaceous fungi and *N. sanguinea* for 'similar' perithecia developing on wood. Seaver also stated that the spore ratio of length to breadth was three to one in *N. sanguinea* and two to one in *N. episphaeria*.

Höhnelt (1912), Weese (1912, 1916, and 1918), Wollenweber (1931), and Petch (1938) considered them to be the same species.

Bolton (1789) described *Nectria sanguinea* as growing on putrid wood and made no mention of Sphaeriaceous fungi as a possible substrate. As there is no known material of Bolton's in existence one can only guess what fungus he had from the somewhat inadequate description. I have never found *N. episphaeria* growing on anything but Sphaeriaceous fungi.

Exsiccata issued as *Sphaeria* or *Nectria sanguinea* do not help as most of those examined by me were either *N. episphaeria* or non-stromatic members of the *N. coccinea* group.

#### *Exsiccata of Nectria sanguinea and their Current Disposition*

Fries, Scler. Suec. (1820) 127 *Sph. sanguinea* = *N. episphaeria*

Fries, Scler. Suec. (1822) 264 *S. sanguinea* = *N. episphaeria*

Baxter, Stirpes Crypt. (1825) 75 *S. sanguinea* = *N. coccinea*

Thümen, Myc. Univ. (1876) 566 *N. sanguinea* = *N. coccinea*

Vize, Microfung. Brit. (1880) 270 *N. sanguinea* = *N. episphaeria*

Ellis, N. Amer. Fung. (1881) 573 *N. sanguinea* = *N. flavo-viridis*

Plowright, Sph. Brit., 8 *N. sanguinea* = *N. punicea* var. *ilicis*

Sydow, Myc. Germ., 694 *N. sanguinea* = *N. coccinea*

I consider that there is little evidence for using the name *Nectria sanguinea*, especially for collections on Sphaeriaceous fungi. *N. episphaeria* was described by Tode as occurring on Sphaeriaceous fungi. The Tode specimen in Herb. Persoon No. 910, 267-659 agrees with Fries' description and is taken as the lecto-type of the species.

#### DESCRIPTION

Perithecia are scattered to gregarious on the surface of effete perithecia or on stroma of sphaeriaceous pyrenomycetes. They are 125-140 (110-200)  $\mu$  in diameter, ampulliform with a short apical papilla, bright red to carmine red, with a smooth semitransparent wall. They develop on a thin byssus, or cushion of

pseudoparenchyma, which generally forms over the ostiole of the host. When fresh they are ovate with an apical disc  $35-45\ \mu$  in diameter and a small central, slightly sunken, ostiolar papilla. When dry they show a pinched collapse involving the apical disc. In section the lateral wall is  $18-22\ \mu$  wide; lining the perithecial cavity are 3-4 layers of hyaline and very thin-walled cells,  $16-24 \times 1-1.5\ \mu$ . Apart from these cells the wall is largely undifferentiated, but it shows

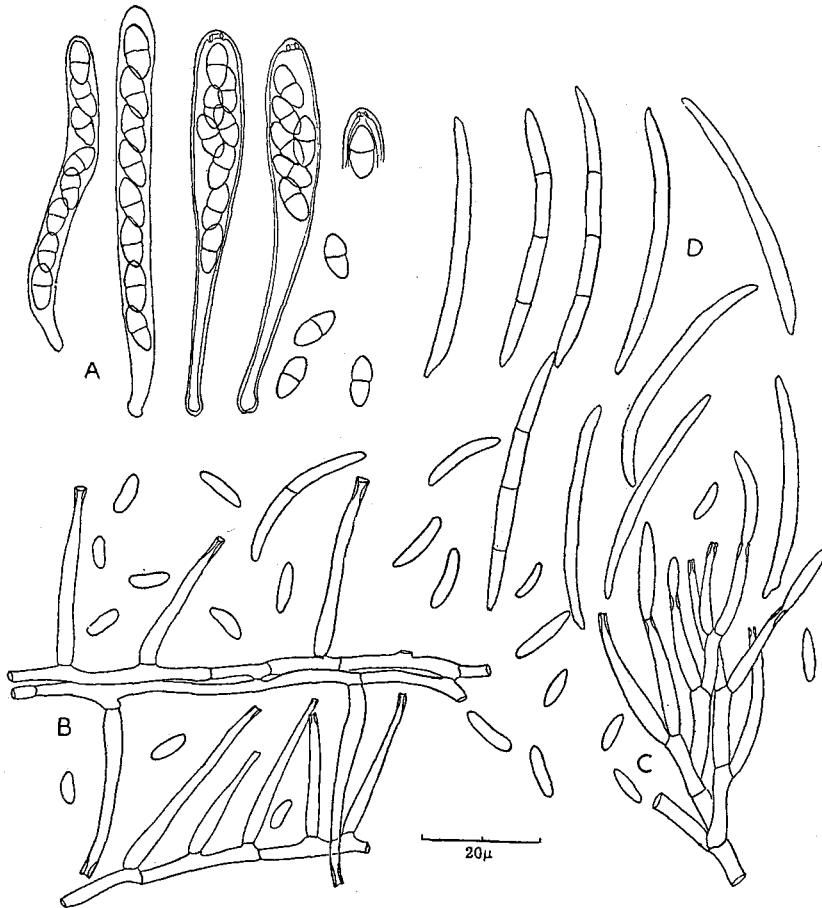


FIG. 23. *Nectria episphaeria*. A, asci and ascospores; B, microconidia and conidiophores; C, macroconidiophores; D, macroconidia.

a gradation from the very thick-walled globose cells,  $3-5\ \mu$  in diameter, of the outer layers to the thinner-walled elongate cells of the inner layers which measure  $5-10 \times 2.5-4\ \mu$ .

The asci are cylindrical to clavate with an apical ring and measure  $56-70 \times 5-6\ \mu$ ; when young they have eight obliquely monostichous ascospores but these become distichous later and occupy the upper  $30-35\ \mu$  of the ascus which now measures  $9-10\ \mu$  wide.

The ascospores are smooth, oblong to ellipsoid, slightly constricted at the central septum and hyaline but becoming light brown and verrucose with age, they measure  $8.5 \times 4\ \mu$  ( $7-11 \times 3.5-5\ \mu$  = range of 200 ascospores from 20 collections).

## CULTURES

Single ascospores isolated on to potato dextrose or malt agar in test-tubes produced a colony only 5 mm. in diameter after 6 days at 22° C. After 12 days it measured 2 cm. in diameter and the surface was covered with a dense white felty and rather erumpent growth. After 4–6 weeks on potato dextrose agar the surface was powdery and avellanaceous but slimy below the mycelium due to conidial formation. On malt agar mycelium formation was much reduced and the surface of the colony was slimy with conidia. Little discoloration occurred except darkening with age.

Microconidia began to develop in 2–4 days from simple lateral phialides on the superficial hyphae. These phialides are hyaline, subulate, and unbranched, they measure 24–35  $\mu$  long and 2–3  $\mu$  at the base narrowing at the apex to 1–1.5  $\mu$  where the lateral wall is thickened to form a collar.

The conidia are hyaline, cylindrical, oval, 6–9  $\times$  2–3  $\mu$ . The formation of macroconidia was considerably influenced by the media and was most prolific on 2 per cent. malt agar on which they develop in abundance after 2–4 weeks.

Macroconidia are falcate with 2–5 indistinct transverse septa. The apex is obtuse and the base is formed of a *Fusarium*-type foot cell; they measure 35–50  $\times$  2.5–3.5  $\mu$ .

## SPECIMENS EXAMINED

*Herb. Lugd. Bat. (Herb. Persoon)*

*Sphaeria episphaeria* (scripsit Tode) dedit Tode (scripsit Pers.) on *Diatrype stigma* on partially decorticated twig No. 910, 267–659 (Lectotype).

*Herb. Uppsala ex Herb. Fries*

*Sphaeria episphaeria* Auct. Fr. Scler. Suec. No. 127 on pyreno on *Fagus*.

*Nectria episphaeria* folder Herb. R.B.G. Kew

Fries, Scler. Suec. 265 (1822), *S. episphaeria* Tode (2 parts). Desm., Crypt. Fr. ser. 1, 972 (1839), *Nectria episphaeria*; Fuckel, Fung. Rhen. 981 (1864), *N. episphaeria*; Ravenel, Fung. Amer. Exs. 340 (1879), *N. episphaeria*; Ellis, North American Fung. 158 (1879), 2422 (1890), 2530 (1891), *N. episphaeria*; O. Jaap, Fung. Sel. 10 (1903), *N. episphaeria*; Tranzschel et Sereb., Mycoth. Rossica 119 (1911), *N. episphaeria* (Tode) Fr. 2 parts; Sydow, Mycotheca germ. 1592 (1921), *N. sanguinea* (2 parts); Seaver and Waterston, Fungi of Bermuda 94 (?1945), *N. episphaeria*.

*Nectria viticola* folder Herb. R.B.G. Kew

Ex Herb. Berk., 5225 *Nectria viticola* B. & C. Alabama.

*Nectria sanguinea* folder Herb. R.B.G. Kew

Fries, Scler. Suec. 127 *Sph. sanguinea*, xii (1820) and 264 *S. sanguinea*, xxvii (1822); Baxter, Stirpes Crypt. Oxen 11, 75 *Sph. sanguinea* (1825); Vize, Micro. Fung. Brit. 270, *N. sanguinea* Fr. iii (1880).

*Incorrectly named Exsiccata in Nectria episphaeria Folder in  
Herb. R.B.G. Kew*

- Baker, Fung. Malayana 166 *N. episphaeria* = *N. ochroleuca*  
 Californian Fung. ex. Herb. Calif. 276 and 277 *N. episphaeria* = *N. coccinea*  
 Petrak, Flora Moravia *N. episphaeria* = *N. purtonii*  
 Rabenhorst, Fung. europaei 262 and 642 *N. episphaeria* = *N. aurantiicola*  
*N. episphaeria* = *N. purtonii*  
 Rehm, Ascomyceten 585 *N. episphaeria* = *N. purtonii*  
 Sydow, Mycotheca March, 1545 *N. episphaeria* = *N. purtonii*

*Nectria episphaeria* folder Herb. I.M.I.

Ex. Herb. Ehrlich. On effete pyrenos: On *Acer*, Saintsbury, Glos., C. G. C. Chesters, May 35 (52151). On *Corylus*, Saintsbury, Glos., C. G. C. Chesters, Nov. 34 (51955). On *Fagus*, Scania, Sweden, J.E., April 34 (51949, 51952, 51953, 51957); Sjaelland, Denmark, J.E., April 34 (51950); Friedrichsruh, Hamburg, Germany, J.E., April 34 (51948). On indet. hosts. Saintsbury, Glos., C. G. C. Chesters and J.E., Nov. 34 (51954). On *Diatrype stigma* on *Acer*, Park Cwn, Gower, S.J.H., Aug. 46 (6157d); Kingthorpe Woods, Yorks., W.G.B., May 54 (56767b); Forge Valley, Yorks., C.B., April 55 (59900); Kingthorpe Woods, Yorks., W.G.B., May 55 (60364); East Bergholt, Suffolk, C.B., May 55 (63130); Bolton Abbey, Yorks., W.G.B., April 56 (62741); Bramham Pk., nr. Leeds, W.G.B., April 58 (72845). On *Crataegus*, Great Hampden Common, Bucks., M. B. & J. P. Ellis, Sept. 49 (37698); Howdale, Yorks., W.G.B., Mar. 58 (72330); nr. Abbotsbury, Dorset, S.M.F., April 58 (73016). On *Fagus*, Boxhill, Surrey, S.J.H., Nov. 46 (6679), Selworthy, Somerset, R. McAleer, May 57 (69519); Ranmore Common, Surrey, C.B., Mar. 58 (72628). On *Fraxinus*, Wheatfen Broad, Norfolk, E.A. & M.B.E., April 47 (14508a); Kingthorpe, Yorks., W.G.B., Nov. 57 (71011a). On *Prunus*, Ranmore Common, Surrey, C.B., Nov. 55 (61408). On *Quercus*, Winnipeg, Canada, A. H. R. Buller & G. R. Bisby, Nov. 31 (26986); Castle Howard, Yorks., W.G.B., Jan. 56 (61821-22). On *Salix*, Abbotsbury, Dorset, S.M.F., April 58 (73015). On *Ulmus*, Mulgrave Woods, Yorks., C.B., Nov. 53 (73635b); Symonds Yat, Glos., C.B., Sept. 55 (61745). Indet. host, Askham Bog, Yorks., E.W.M., April 48 (360); Grantly Hall, Yorks., C.B., April 54 (56377); Forge Valley, Yorks., C.B., April 55 (60271). On *Anthostoma* on *Fagus*, Gt. Hampden Common, Bucks., M. B. & J. P. Ellis, Sept. 49 (37624). On *Diatrypella* on *Ulex*, Seaford, Sussex, S.M.F., Mar. 56 (62959). On *Eutypa* on *Hedera*, Kingthorpe, Yorks., W.G.B., May 55 (60365). On *Hypoxyylon* on *Fagus*, Stroud Foray, no locality, E.W.M., May 34 (22842). On *Quaternaria* on *Fagus*, Ex Herb. Ludwig, July 21 and June 21 (18372 and 18371); Ranmore Common, E.W.M., Feb. and Mar. 39 (50365 and 50364); Salperton, Glos., E.W.M., Sept. 43 (22844); Arncliffe Woods, Yorks., S.J.H., Sept. 46 (6903). On indet. *pyrenos.* on *Acer*. Bolton Abbey, Yorks., W.G.B., April 56 (62742). On *Fraxinus*, Moulin Huet, Guernsey, M. B. & J. P. Ellis, Sept. 48 (33975).

*Nectria desmazierii* Beccari & de Not., *Erb. Critt. Ital.*, x, No. 983, 1863; de Not., *Sfer. Ital.*, 1, p. 10, 1863.

*Sphaeria sanguinea* var. *cicatricum* Berk. *Mag. Zool. and Bot.*, 1, p. 48, 1837.

*Nectria coccinea* var. *cicatricum* (Berk.) Desm. *Ann. Sci. Nat.*, ser. 3, xx, p. 351, 1848.

*Nectria cicatricum* (Berk.) Tul., Sel. Fung. Carp., iii, p. 77, 1865.

*Nectria gibbera* Fuckel, Symb. Myc., p. 177, 1870. Teste Fuckel, loc. cit. Nact. 1, pp. 21–22, 1871.

*Dialonectria desmazierii* (de Not.) Petch, *Naturalist.*, Lond., p. 281, 1937.

*Fusarium buxicola* Sacc., Teste Wollenweber, *Zbl. Bakt.*, 106, p. 113, 1943.

*Fusarium buxi* Sacc., *Michelia*, 1, p. 300, 1878.

This rarely collected species is restricted to box (*Buxus sempervirens*) in Britain. It is usually found on the leaf scars but it also occurs on the bark and occasionally on the bare wood.

A British collection (I.M.I. 22819) made by Mr. E. W. Mason was grown by Dr. J. Ehrlich and found to produce a *Fusarium* conidial state. Some of these cultures sent to Dr. Wollenweber formed perithecia which he stated were identical with Fuckel's Fung. Rhen. 2357 *Nectria desmazierii*, and the *Fusarium* with Saccardo's *Fusarium buxi*. (Saccardo called the latter *F. buxicola* in 1883.)

#### DESCRIPTION

Conidial formation generally precedes perithecial development. These conidia are formed on sporodochia which develop as a loose byssus over the leaf scars and buds of box. The mycelium forming the byssus is composed of hyaline

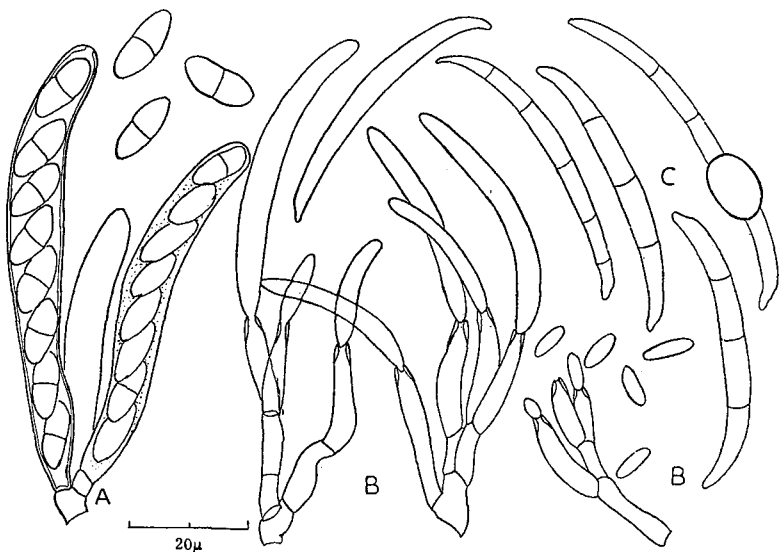


FIG. 24. *Nectria desmazierii*. A, asci and ascospores; B, micro- and macroconidiphores and conidia from host; C, conidia from culture one showing chlamyospore formation.

hyphae with cells  $14-22 \times 2-3 \mu$ . The surface of the sporodochia is covered with phialides  $12-18 \times 3-4 \mu$ . Macroconidia formed from these are *Fusarium*-like and measure  $30-55 \times 4-5 \mu$ ; when mature they have 4–6 transverse septa.

Perithecia form over the conidial sporodochia in groups of up to 30. They are yellow to orange, broadly ovate to globose, with a smooth outer wall and without a marked ostiolar papilla. They measure  $120-175 \mu$  in diameter and on drying

show an irregular lateral collapse. In section the lateral wall is 22–30  $\mu$  wide and shows a gradation from the thick walled outer cells to the very thin walled cells lining the perithecial cavity. The outer cells are ovate to globose 8–10  $\times$  6–8  $\mu$  whilst those lining the perithecial cavity are fusoid 8–11  $\times$  2.5–4  $\mu$ .

The asci are cylindrical with a rounded slightly thickened apex bearing a thinner central region or pore, there is no thickening or ring formation; they measure 65–80  $\times$  7–9  $\mu$ , and have eight obliquely monostichous ascospores.

Ascospores are smooth hyaline, ellipsoid with a slight constriction at the single central septum. They measure 12–16  $\times$  5–7  $\mu$ .

#### CULTURES

As stated, the only British collection of this species to be cultured was grown by Dr. J. Ehrlich. The following description of cultural characters is from his notes in Herb. I.M.I.

Ascospores were isolated on to potato dextrose, malt, and prune agar. The colonies were pure white with dense aerial mycelium but soon yellowish-white pinnotes of *Fusarium* conidia developed in all tubes. (Wollenweber states in litt. that perithecia developed on oatmeal agar after 3 months.)

The first conidia to form were microconidia which arose on short lateral phialides on the hyphae, they were hyaline, ellipsoid and measured 6–8  $\times$  2–2.5  $\mu$ . Macroconidia, formed in 7–9 days on small stromatic pustules, were curved cylindrical with a pointed apex and a *Fusarium* like foot cell; they had 3–6 septa and measured 45–60  $\times$  3–5  $\mu$ . Globose chlamydospores occasionally formed from the cells of the macroconidia in older cultures.

These isolations are deposited in Herb. I.M.I. with the host material and have been examined by me.

#### SPECIMENS EXAMINED

*Nectria desmazierii* folder Herb. R.B.G. Kew

*Nectria desmazierii* ex Herb. Critt. Ital. (This is a fragment of the authentic material issued by Beccari and de Not. in Erb. Critt. Ital., xx, No. 983, 1863, and sent to Cooke. Perithecia and *Fusarium* sporodochia are present. A further slide now in Herb. I.M.I. made by Dr. Ehrlich from Fries' herbarium at Upsala agrees with this material.) *Sph. sanguinea* var. *cicatricum* Berk. (Brit. Fung. Fasc. 2, 83, 1836). Fuckel, Fung. Rhen. Ex. Suppl., ix, 2357 (1871), *N. desmazierii*. Saccardo, Mycoth. Ven. 116 (1874), *N. desmazierii*. Thümen, Fung. Aust. 962 (1873), *N. gibbera*.

*Nectria desmazierii* folder Herb. I.M.I.

On *Buxus*, Overstrand Woods, nr. Norwich, Norfolk, E.W.M., Oct. 34 (22819); Silent Pool, Shere, Surrey, B. A. Stone, Nov. 52 (50686d).

*Nectria magnusiana* Rehm ex Sacc., *Michelia*, 1, p. 294, 1878. (Rehm in Ber. Naturhist Ver Augsburg, xxvi, 1881 and *Hedwigia*, xxi, p. 59, 1882.)

*Dendrodochium epistroma* (Syd.) Höhn, *S.B. Akad. Wiss. Wien*, 1, cxviii, p. 424, 1909.

*Hymenula epistroma* Syd. 'nomen nudum', Syd. Mycoth. Germanica No. 648.

Rehm used the name *Nectria magnusiana* for his Ascomyceten exsiccatum No. 436, 1878, issued without a diagnosis. This was published by Saccardo in July 1878 and later by Rehm (1881).

I have had no fresh collections of this from which the ascospores would germinate. Wollenweber confirmed the conidial state as *Dendrodochium epistroma* (Syd.) Höhn. and the available evidence indicates this to be correct.

Allescher (1895) published *Fusarium magnusiana* and referred to it as conidial *Nectria magnusiana* citing Fungi Bavar. Exs. iv, No. 400, 1894. I have not seen any example of this exsiccatum. Wollenweber (1931) believed it to be an associated fungus and placed it as a synonym of *F. aquaeductuum* Lagh. v. *pusillum* Wr. stat. conid. of *N. moschatae* Gluck.

The actual conidial state was published by Höhnelt (1909) as *Dendrodochium epistroma* based on Sydow's Myc. germ. 648 *Hymenula epistroma*. He said that it suggested itself as the conidial fructification of *N. magnusiana* although he could not find it on his examples of this species. Otto Jaap published his Fungi selecti No. 418 in 1910 as *N. magnusiana* on *Diatrypella favacea* on *Betula alba*, associated with its conidial state *Dendrodochium epistroma*. Wollenweber (1931) agreed with this. Examination of Sydow's exsiccatum 648 shows it to be identical with the *Dendrodochium* associated with *N. magnusiana*.

W. B. Groves's reference to *Tremella aurantiaca* as conidial *Nectria magnusiana* reflects the old use of the name *Tremella* for gelatinous fungi (*Tubercularia vulgaris* was called *Tremella purpurea* by Linnaeus). The mass of conidia of *N. magnusiana* appear gelatinous when moist. It is difficult to understand on what species the name was based. In Weinmann's publication (1836) it is cited as *T. aurantiaca* Schweinitz. Saccardo refers to it as a synonym of *T. elegans* which is a Basidiomycete.

*Nectria magnusiana* is readily distinguished from all other *Nectrias* on its host relationship. *N. purtonii* and *N. wegeliniana* are the two most closely allied species. Apart from habitat, *N. magnusiana* can also be distinguished from the former by its larger ascospores and smaller conidia and from the latter by its smooth-walled and smaller ascospores. The conidial state of *N. wegeliniana* is not known and no authentic collection of the species has been found in Britain.

#### DESCRIPTION

The conidial fructifications develop before the perithecia and are densely crowded on a weakly developed stroma. This may be convoluted in places and the whole surface is covered with branched conidiophores. Each branch terminates in a narrow subulate phialide which measures  $12-20 \times 1.5-2 \mu$ . These produce hyaline, allantoid conidia,  $4.5-6 \times 1.5-2 \mu$ .

Perithecia form later on the same stroma but are so densely aggregated that this is obscured. They are globose, yellowish red, with a smooth outer wall and a large flat apical disc. They are translucent when young but become darker with age when they undergo a pomiform, or less frequently a lateral, collapse; they measure  $250-350 \mu$  in diameter. In section the wall is  $48-55 \mu$  wide with two distinct regions. The outer,  $24-32 \mu$  wide, has globose cells  $4-5 \mu$  in diameter with thick reddish-yellow cell walls. The outer layers of cells have thicker walls than the inner layers. The inner region measures  $20-26 \mu$  wide and is composed



of thin-walled hyaline cells that become crushed as the asci mature, they measure  $9-12 \times 2-3 \mu$ .

The asci are cylindrical to narrowly clavate with a rounded apex bearing an

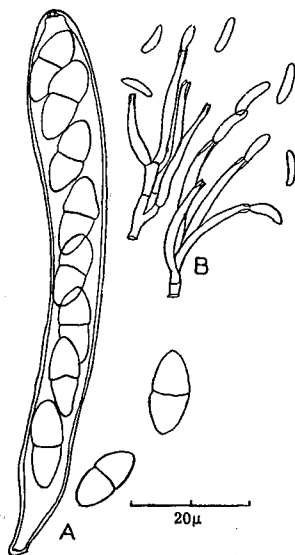


FIG. 25. *Nectria magnusiana*. A, asci and ascospores; B, conidiophores and conidia from host.

apical pore; they measure  $72-84 \times 9-12 \mu$  and have 8-obliquely monostichous ascospores.

Ascospores are broadly fusoid to ellipsoid, smooth walled, hyaline, becoming light brown, and measure  $10-15 \times 4.5-6 \mu$ .

#### SPECIMENS EXAMINED

*Nectria magnusiana* folder Herb. R.B.G. Kew

Rehm, Ascomyceten 436 (1878), *Nectria magnusiana* on *Diatrypella favacea* (authentic for name); O. Jaap, Fungi selecti exs. 418 (1910), *N. magnusiana*; (Brit. coll.) *N. episphaeria* on *Diatrypella quercina* on *Quercus*, Carlisle, Dr. Carlyle, 1884, probably the first British record. On *Diatrypella* on *Betula*, Aberford, Yorks., W.G.B., Jan. 9 and Oct. 9, 1938.

*Hymenula epistroma* folder Herb. R.B.G. Kew

Sydow, Mycoth. germ., 648 *Hymenula epistroma* on *Diatrypella favacea*, Brandenburg, P. Vogel, Nov. 1906.

*Nectria magnusiana* folder (Brit. coll.) Herb. B.M. Nat. Hist.

On *Diatrypella* on *Betula*, Rehm, Ascomyceten 436 (1878); Logan Woods, nr. Sandhead, Wigtownshire, Aug. 36; Aberford, Yorks., W.G.B., Oct. 37.

*Nectria wegeliiana* folder (Brit. coll.) Herb. B.M. Nat. Hist.

On *Diatrypella* on *Betula*, Lytchett, H. C. Hawley, Oct. 22. On *Diatrypella* on *Quercus*, Logan Woods, Wigtownshire, C. G. C. Chesters, Aug. 36.

*Nectria magnusiana* folder Herb. I.M.I.

On *Diatrypella* on *Betula*, Dunbartonshire, Scotland, C. G. C. Chesters and J.E., Mar. 35 (22829); Oxshott, Surrey, G. R. Bisby, Nov. 38 (18357); Bramham Park, Yorks., W.G.B., April 58 (73355).

***Nectria purtonii*** (Grev.) Berk., *Outlines Brit. Fung.*, p. 394, 1860.

*Sphaeria purtoni* Grev., *Scot. Crypt. Fl.*, vi, Synopsis 23, 1828.

[*Cucurbitaria pinastri* Grev., *Scot. Crypt. Fl.*, i, pl. 50, 1823 (pro parte).]

*Nectria applanata* Fuckel, *Symb. Myc.* (Nacht. 1), p. 22, 1871.

*Dialonectria applanata* (Fuckel) Petch, *Trans. Brit. mycol. Soc.*, xxv, p. 170, 1941.

*Stylonectria applanata* Höhn., *S.B. Akad. Wiss. Wien*, I, cxxiv, p. 52, 1915 (p. 4 in sep.)

When Greville (1823) described *Cucurbitaria pinastri* his description was based in part on a *Nectria* and in part on a *Valsa* on which the *Nectria* was growing. Greville presumably sent part of his material to Fries as in 1828 Fries wrote that it was the same species as *Sphaeria abietis* (now *Valsa abietis*). Fries said that the red ostioles described by Greville belonged to *Sph. episphaeria*. By this time Greville (1828) was aware of his mistake because he redescribed the *Nectria* as *Sph. purtoni*. *Sph. pinastri* had already been used for a *Valsa* (Fries, *Syst. Myc.* ii, p. 488, 1823). Currey (1858) redescribed *Sph.* (*Nectria*) *purtoni* Grev. but as Currey's citation is not regarded as a nomenclatorial combination, the name *Nectria purtonii* must date from Berkeley's (1860) publication.

When Fuckel (1871) described *Nectria applanata* he stated that pycnidia developed with the perithecia, both were similar in appearance and in type of spore produced except that the pycnospores were a little larger.

Weese (1916) agreed with Fuckel, he did not mention the ascospore size but said they were similar to the pycnospores only smaller. Höhnel (1915) erected the genus *Stylonectria* for these pycnidia and named the species *S. applanata*.

From an examination of sections of Fuckel's material in Herb. R.B.G. Kew I found that the bodies referred to by Fuckel as pycnidia are in fact perithecia in which the ascospores have been retained and the asci have disintegrated. No conidiophores are present in these perithecia and the wall structure is identical with that of perithecia-bearing asci. It would be unusual, to say the least, to find a pycnidium with a structure identical with the perithecium within the Nectriaceae.

*Spore measurements of 'Pycnospores' and Ascospores of N. applanata*

Author or material	Date of publication	'Pycnospores'	Ascospores in asci
Fuckel . . . . .	1871	12-14 × 4-5 μ	8 × 4 μ
Weese . . . . .	1916	10-14 × 4-4.5 μ	..
Petch . . . . .	1938	9-12 × 4-4.5 μ	8-10 × 3.5-4 μ
Ex. Fuckel (Herb. Kew) . . . . .	..	(Free ascospores)	..
Fung. Rhen. 2356 . . . . .	..	9-12 × 4 μ	8-10 × 3.5-4 μ

The variation between the 'pycnospores' (the free ascospores) and the ascospores in asci is no greater than would be expected. Cultures from fresh collec-

tions of this species form *Fusarium* conidia closely related to other species in this group of *Nectria*.

## DESCRIPTION

In the early stages of development of the *Nectria* a thin stromatic layer forms over the ostioles of effete, generally valsoid, Sphaeriaceous fungi. This stroma is covered early with a palisade of short hyaline conidiophores, these form

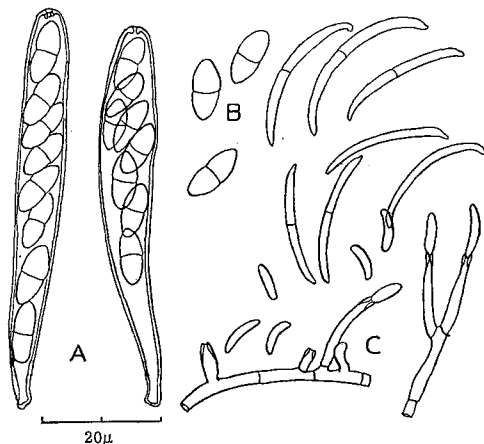


FIG. 26. *Nectria purtonii*. A, asci and ascospores; B, conidia from host; C, conidia and conidiophores from culture.

hyaline, allantoid to fusiform conidia that become 1-septate and measure  $9-16 \times 2-2.5 \mu$ . Perithecial initials form in or on the surface of this stroma which is almost obscured as they develop.

The densely crowded perithecia are yellow to red with a smooth wall which appears semi-transparent. The shortly ampulliform neck with a flat or concave top is characteristic. When dry a slight lateral collapse occurs in the lower half of the perithecium; they measure  $150-230 \mu$  in diameter. In section the lateral wall is  $38-42 \mu$  wide and formed of two regions. The outer,  $20-26 \mu$  wide, is composed of thick-walled globose cells  $6-7 \mu$  in diameter in which the lumen is almost obscured. The inner layers are formed of elongate cells,  $10-12 \times 3-4 \mu$ , with much thinner walls.

Asci are  $55-70 \times 6-9 \mu$ , cylindrical to narrowly clavate with a rounded apex containing an apical ring, the eight ascospores are obliquely monostichous becoming distichous.

The hyaline ascospores have obtuse ends giving them an almost cylindrical shape, but when mature they are slightly constricted at the central septum and light brown in colour; they measure  $8-11 \times 3.5-4.5 \mu$ .

## CULTURES

Cultures developing from single ascospore isolations showed very slow growth and after 6 weeks extended only 1.5 cm. along the agar slope. The surface of the colony was covered with a sparse white floccose mycelium with a pale yellowish-brown erumpent mass at the point of the inoculum, which developed a

slimy appearance as the conidia were produced. The agar showed a slight yellow-brown discoloration.

Conidia began to form on potato dextrose and malt agar after 4–5 days at room temperature in the light. The first-formed conidia, developed from short lateral phialides on the hyphae, were hyaline, allantoid  $5-7 \times 1.5-2 \mu$ .

Macroconidia which developed later were fusoid,  $20-24 \times 1.5-2 \mu$  usually with a single central septum. Conidiophores were not well developed in culture and did not form a synnema.

#### SPECIMENS EXAMINED

*Nectria applanata* folder Herb. R.B.G. Kew

Fuckel's Fungi Rhen. 2356 *Nectria applanata* Fuckel on *Carpinus* (type coll.). Two other parts of this issued as Herb. Berbey-Boissier 862. Sydow, Mycotheca germanica 2137 *Nectria applanata* Fuckel on *Betula* coll. Ludwig.

*Nectria purtonii* folder Herb. R.B.G. Edinburgh

*Cucurbitaria pinastri* Grev. = *Nectria purtoni* (Grev.) Curr., Rosslyn Woods, 1820 (co-type coll.). *Sphaeria purtoni* Grev. Cr. Fl. Synops (no other data).

*Nectria purtonii* folder Herb. I.M.I.

On *Acer* ex Herb. Ludwig, sub. *N. sanguinea*, Flora von Westfalen, June 23 (18370); on *Alnus*, Ellerburn, Thorton Dale, Yorks., W.G.B., April 57 (69074); Shoshone Co., Idaho, U.S.A., J.E. and R. K. Pierson, June 36 (51958); on *Betula*, Benmore Estate, Argyllshire, J.E. & C. G. C. Chesters, Mar. 35 (51956).

*Nectria leptosphaeriae* Niessl in Krieger, Fung. Saxonici, iv, No. 165, 1886 (Rehm, *Hedwigia*, xxvi, p. 92, 1887).

*Nectria leptosphaeriae* Niessl var. *macrospora* Wr., *Ang. Bot.*, viii, p. 187, 1926.

*Hypomyces leptosphaeriae* (Niessl) Wr., *Ann. mycol. Berl.*, xv, p. 8, 1917.

*Sphaerostilbe flammeola* Höhn., *S.B. Akad. Wiss. Wien*, 1, cxxiv, p. 2, 1915.

*Lasionectria leptosphaeriae* (Niessl) Petch, *Trans. Brit. mycol. Soc.*, xxi, p. 268, 1938.

*Fusarium sphaeriae* Fuckel, *Symb. Myc.*, p. 370, 1870; Fung. Rhen. No. 212.

*Fusarium sphaeriae* Fuckel var. *majus* Wr., *Fus. Auto. Del.* No. 859, 1930.

Petch (1938) placed *Nectria leptosphaeriae* in the genus *Lasionectria*. I failed to find any true hairs on the perithecia which I examined, including the collections cited by Petch. Hyphae on the lower part of the venter are derived from the byssus and are not true hairs.

Wollenweber (1926) described *Nectria leptosphaeriae* var. *macrospora* with the conidial state as *Fusarium sphaeriae*, he said that it differed from *N. leptosphaeriae* in having larger ascospores and smaller conidia. Ten years before, Weese (1916) stated that the spores of the type material were larger than in the original description, and in 1935 Wollenweber withdrew his var. *macrospora* as he now considered it to be part of the species *N. leptosphaeriae*.

## DESCRIPTION

Perithecia dispersed amongst and occasionally seated upon the perithecia of *Leptosphaeria acuta* and *L. dobiolum* on *Urtica*. No stroma is present although they may be seated upon a thin loose byssus. They are smooth walled, orange to

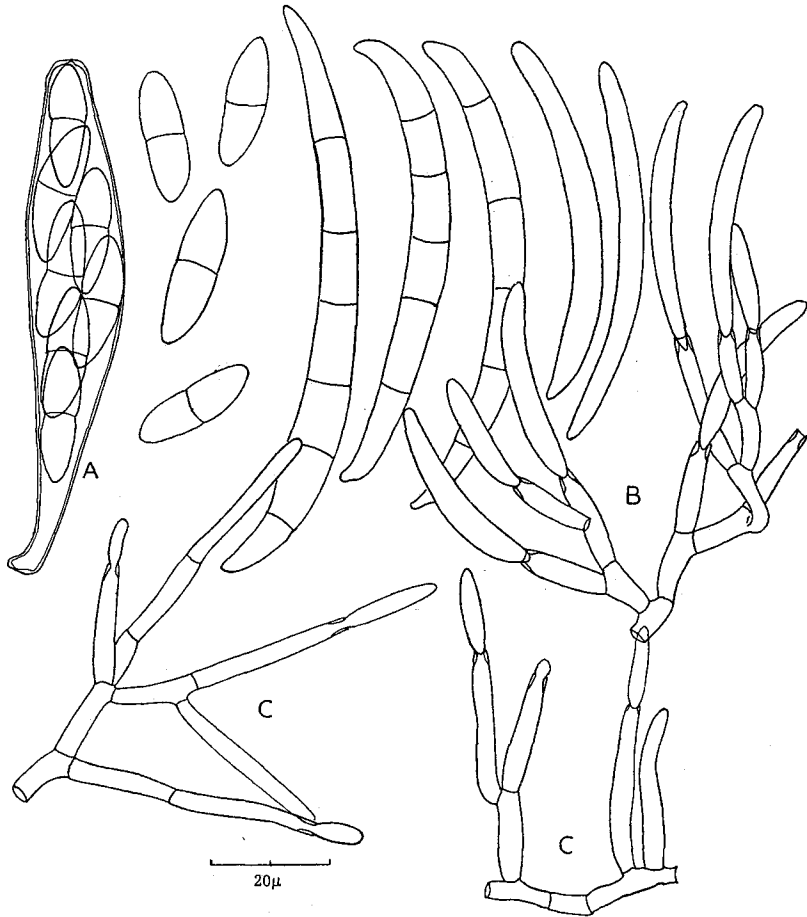


FIG. 27. *Nectria leptosphaeriae*. A, asci and ascospores; B, conidia and conidiophores from host; C, conidiophores from 7-day culture on malt agar.

red, ampulliform with a short neck, and show lateral collapse when dry; they measure  $280\text{--}375\ \mu$  in diameter. In section the lateral wall is  $22\text{--}30\ \mu$  wide. The outer cells are thick-walled, sub-globose to elongate,  $14\text{--}20 \times 3\text{--}9\ \mu$ , but the walls become progressively thinner towards the inner layers. Lining the perithecial cavity are several layers of very thin-walled elongate cells  $9\text{--}15 \times 2\text{--}3.5\ \mu$ .

The asci are cylindrical to clavate with eight obliquely monostichous to sub-distichous ascospores, the apex is rounded with a thickening in the centre of the apex forming a ring.

The ascospores are broadly fusiform to ellipsoid and slightly constricted at the central septum; they measure  $18\text{--}26 \times 6\text{--}8\ \mu$  and when mature turn light brown.

Conidia develop before, and in a similar position to, the perithecia on a loose byssus, a small pulvinate stroma, or on the pycnidia of the *Leptosphaeria*. The conidiophores are dichotomously branched and each branch terminates in a phialide  $14-24 \times 3.5-4 \mu$ . These are cylindrical but slightly constricted at the apical collar.

Conidia are *Fusarium*-like but the foot cell is often indistinct; they measure  $57-67 \times 4-6 \mu$  and become 3-5 septate when mature. In mass they are pink to greyish white.

#### CULTURES

The ascospores isolated on to potato dextrose agar, potato starch agar, and malt agar gave rise to slow-growing cultures. After 3 weeks the colony was 1-1.5 cm. in diameter and erumpent in the centre. The surface was covered with white floccose hyphae which became felted and then slimy in appearance as the conidia developed. These were formed after 5-7 days from lateral phialides on the hyphae; they are  $20-30 \mu$  long and  $2.5-3 \mu$  at the base narrowing towards the apex where the lateral wall is thickened to form a collar. After 7-10 days the phialides are borne terminally on branched conidiophores and finally after about 3 weeks as a palisade of short doliform phialides covering the surface of small pinnotes or sporodochia.

The conidia are curved, cylindrical, occasionally swollen towards the rounded or angular apex and terminating basally in a fusarium foot cell; they are 4-6 septate when mature and measure  $70-95 \times 5-8 \mu$ .

#### SPECIMENS EXAMINED

*Nectria leptosphaeriae* folder Herb. B.M. Nat. Hist.

Krieger, Fungi Saxonici iv, No. 165 (1886), *Nectria leptosphaeriae* Niessl, Oct. 1885 (type coll.). *Nectria* on nettle, Batheaston, Nov. [18]61 Ex Herb. Broome No. 292 *N. leptosphaeriae*. This is probably the first British record.

*Nectria leptosphaeriae* folder Herb. R.B.G. Kew

Rehm, Ascomyceten 880 (1886), *Nectria leptosphaeriae* Niessl; Rabenhorst No. 3442 (1886), *Nectria leptosphaeriae*; Tranzschel et Serebrian, Mycoth. Rossi, No. 268 (1912), *Nectria leptosphaeriae*; Otto Jaap, Fungi selecti Exs. No. 465 (1911), *Nectria leptosphaeriae* Niessl.

*Fusarium sphaeriae* folder Herb. R.B.G. Kew

Fuckel, Fung. Rhen. No. 212 (1863), *Fusarium sphaeriae* Fuckel on *Sph. dolium* on *Urtica*.

*Nectria leptosphaeriae* folder Herb. I.M.I.

On *Leptosphaeria* sp. on *Urtica*, Carr near Mystery Pool, Wheatfen Broad, Norfolk, E.A.E., Dec. 40 (72275); Old Lakenham, Norfolk, E.A.E., Jan. 42 (74246); Clumber Park, Worksop, Notts., J.W., Nov. 58 (75333).

*Nectria flavo-viridis* (Fuckel) Wollenweber, *Angew. Bot.*, viii, p. 186, 1926.

*Sphaerostilbe flavo-viridis* Fuckel, *Symb. Myc.*, Nacht. 1, p. 22 (310), 1871.

In the authentic material examined, numerous small yellow *Stilbum*-like synnemata are associated with the perithecia. They are fragile, pale yellow, and

400–600  $\mu$  high with a stipe 56–65  $\mu$  wide which spreads out at the apex to form a knob 220–250  $\mu$  in diameter. Phialides covering the upper surface of the knob measure 14–20  $\times$  1.5–2  $\mu$ . Conidia formed from these are hyaline, 1-septate, fusi-form with a broader apex than base and usually slightly curved. They measure 12–17  $\times$  2–3  $\mu$ . The larger conidia mentioned by Fuckel occur in abundance in culture.

Wollenweber (1935) gave the spores as 10.1  $\times$  4.7 (7.5–13  $\times$  4.5–5)  $\mu$ , but in the collection made by Mr. Mason and confirmed by Wollenweber the average spore size is 12.8  $\times$  5.6  $\mu$  and this spore size is very close to that found in the other collections cited.

Weese (1916) stated that the perithecia of *Nectria flavo-viridis* were indistinguishable from those of *N. sanguinea* (Bolt ex Fr.) Fr. I can find no justification for retaining the name *N. sanguinea*, as there is no proof of the identity of the species to which the name was first applied.

*Nectria flavo-viridis* is separated from *N. epispheeria* and *N. viridescens* on the larger ascospores and perithecia. In culture, the green coloration separates it from *N. epispheeria*, and the *Fusarium* conidia from *N. viridescens*.

#### DESCRIPTION

The perithecia develop on the surface of the host, or on the surface of effete carbonaceous pyrenomycetes. They are ampulliform with a smooth outer wall and a short neck that is darker than the venter and possesses a minute central ostiole. The colour varies from light red to deep brownish red with the apical papilla becoming almost black. When effete the upper half of the perithecium collapses into the lower half with the papillate ostiole remaining upright in the centre; lateral collapse may also occur and this involves the upper half of the perithecium only.

In section the lateral wall measures 22–24  $\mu$  wide and consists of 5–6 layers of thick-walled elongate cells 11–14  $\times$  4.5–6  $\mu$  interspersed with globose cells 5–7  $\mu$  in diameter. The only wall differentiation that exists is that formed by the 3–4 layers of very thin-walled elongate cells that line the perithecial cavity, which become crushed as the asci mature.

The asci are cylindrical with a rounded apex possessing a pore and with a short flattened base, they measure 85–104  $\times$  7.5–9  $\mu$ , and have eight monostichous or sub-distichous ascospores.

The oval ascospores are slightly constricted at the single central septum, when hyaline they measure 10–16  $\times$  5  $\mu$  but as they mature they turn light brown and on discharge measure 12–16  $\times$  5–8  $\mu$ .

#### CULTURES

Single ascospores isolated on to malt, maize meal, and potato dextrose agar in test-tubes showed a marked difference in growth and colour. After 14 days at room temperature and in the light the superficial mycelium covered about two-thirds of the surface of the agar in test-tubes. On malt agar the aerial mycelium was sparse and only a pale green discoloration of the agar was present; micro- and macroconidial production was abundant and aggregations of these formed slimy pink pustules. Mycelium was also formed sparsely on maize meal

agar but the surface remained dry and conidial production was not so abundant as on malt agar. The agar developed a strong green discoloration. On potato dextrose agar the colony was more erumpent with a white floccose aerial mycelium and a marked green discoloration of the agar.

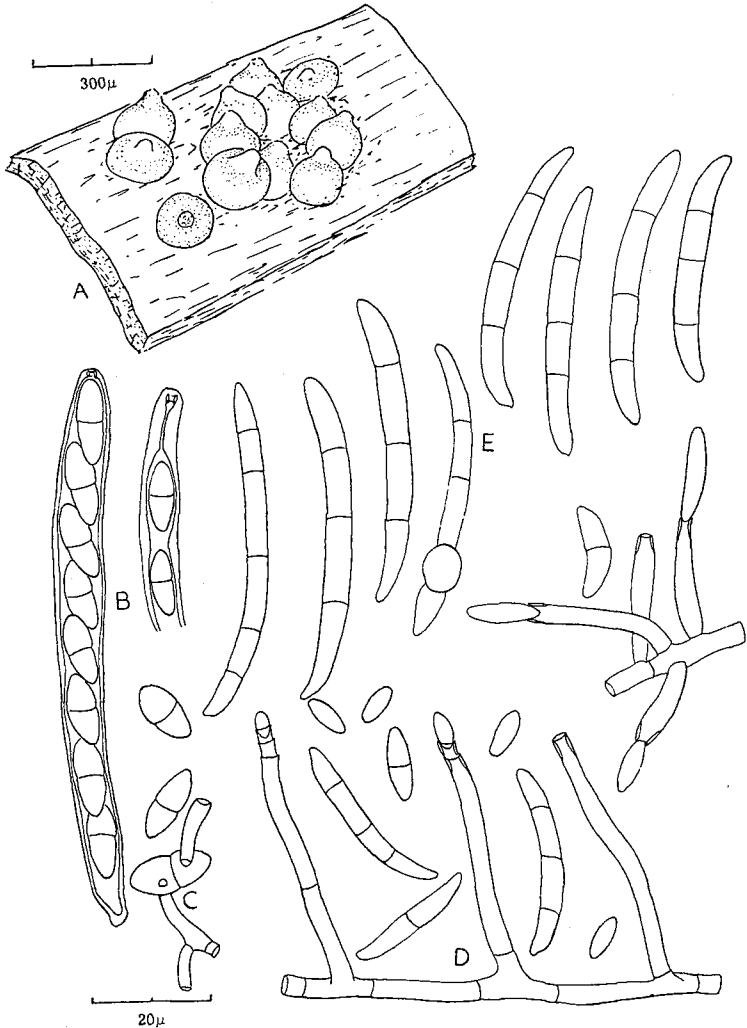


FIG. 28. *Nectria flavo-viridis*. A, habit sketch of perithecia on host; B, asci and ascospores; C, germinating ascospore; D, macroconidia and phialides from 7-day culture; E, conidiophores and conidia from 1-6 months' old cultures on potato dextrose agar.

Conidiophore production began 2-3 days after ascospore germination, the first consists merely of lateral phialides which arise from adjacent cells of the superficial hyphae; these phialides are cylindrical with a local thickening of the wall in the form of a ring just below the apex. After several conidia have been formed production ceases and the inner wall of the phialide grows through the collar region to form another collar at a higher level on the same phialide, the primary collar remains as an annulation. As this process is repeated several annulations



can be seen below the apex of the phialide. This is thought to be a light reaction as it is not found in cultures kept in the dark.

The first conidia are hyaline, broadly fusoid, amerospores,  $7-11 \times 2-3 \mu$  but later from the same phialide conidia are formed that become one-septate before release and measure  $15-25 \times 3-4 \mu$ . These may elongate further, develop 3-5 septa and finally measure  $25-50 \times 3-5 \mu$ , some develop a typical *Fusarium* foot cell.

In older cultures, especially on corn meal agar, the mycelium aggregates to form discrete pseudostromatic pustules  $300-400 \mu$  in diameter, conidial production becomes confined to these stromata and phialides cover the surface. These phialides are shorter and broader than the primary ones and measure  $12-20 \times 3-3.5 \mu$ . The *Fusarium* conidia formed from these are four to six-celled and measure  $48-62 \times 3.5-5 \mu$ . As the cultures dry out, chlamydospores form from the cells of the macroconidia, these are globose, thick-walled, and measure  $7-9 \mu$  in diameter.

## SPECIMENS EXAMINED

*Sphaerostilbe flavo-viridis* folder Herb. R.B.G. Kew

Fuckel's Fung. Rhen. Exs. 2353 (1871), *Sphaerostilbe flavo-viridis* on *Betula*, Co-type.

*Nectria flavo-viridis* folder Herb. I.M.I.

On *Acer*, ex Herb. Ludwig, May 21 (18369); Cleeve Coombe, Bristol, A. H. S. Brown, Sept. 55 (61054c); Gwydyr Forest, Llanrwst, C.B., May 58 (73440). On *Fraxinus*, Woodchester Park, Gloucestershire, E.W.M., May 34 (22820, confm. Wollen.). On *Pinus*, nr. Brandon, Suffolk, J. Rishbeth, Oct. 58 (74992). On *Quercus*, Kingthorpe, Yorks., W.G.B., April 57 (69081). On *Salix*, Portadown, Armagh, C. M. Leach, Feb. 50 (39892); *Indet. bark* Tarr steps, Somerset, R. McAleer, May 57 (69538a).

***Nectria viridescens* spec. nov.**

This species has been collected eight times. In the past it may well have been called *Nectria sanguinea*. However, there is no evidence as to the identity of the fungus on which this name was based. The Fries' *exsiccata* Scler. Suec. Nos. 127 and 264 *N. sanguinea* are predominantly *N. episphaeria* as are most other *exsiccata* examined by me that were issued as *N. sanguinea*. It has been decided therefore to describe this species as new and to consider *N. sanguinea* as a *nomen confusum*.

*Nectria viridescens* is very characteristic in culture and the epithet is taken from the striking green coloration of the mature cultures on 2 per cent. potato dextrose agar.

*Stromata* vestigialia vel nulla.

*Perithecia* rubra, levia, ampulliformia,  $200-250 \mu$  alta,  $150-200 \mu$  diam.

*Asci* cylindrici, basi truncati, apice rotundati et cingulo refringenti porum circumambienti praediti, octospori,  $68-76 \times 6-9 \mu$ .

*Ascosporae* oblique monostichae vel subdistichae, hyalinae vel pallide brunneae, ellipsoideae, 1-septatae, minute verrucosae,  $7.5-10 \times 4-5 \mu$ .

## In Cultura

*Mycelium* album, floccosum, in agaro colorem fuscoviridem efficiens.

*Conidiophora primaria* (sue phialides simplicis) ex hyphis mycelialibus lateraliter oriunde, hyalina, subulata,  $30-45 \times 2-2.5 \mu$ .

*Conidiophora secundaria* in synnematis pallide brunneis,  $300-500 \mu$  longis, aggregata et phialides  $22-45 \mu$  longas,  $2.5-3.5 \mu$  latas, ex ramulis brevibus lateralibus efficiuntia.

*Conidia* hyalina, globosa vel reniformia,  $4-8 \times 2.5-3 \mu$ .

*Habitat* in corticis ligni emortui. Typus in ramis *Salicis*, Sawley Woods, Yorks., C.B., April 54 (I.M.I. 56736).

## DESCRIPTION

The perithecia are scattered to gregarious, on the periderm or exposed wood of deciduous or coniferous trees, the stroma if present is vestigial. They are ampulliform with a short broad neck bearing a conical or flat disc  $45-55 \mu$  in diameter with a central ostiole, when young they are yellow to light red but become darker with age, the neck is lighter or concolourous. The perithecia collapse on drying by invagination of one or both sides of the venter but the apical disc usually retains its shape (a marked distinction from *Nectria epispheeria*). They measure  $150-200 \mu$  in diameter. In section the lateral wall is  $26-40 \mu$  thick and formed of two regions. The outer of these is  $16-22 \mu$ , and has elongated  $7-10 \times 3-4 \mu$  or globose  $5-6 \times 3.5-4 \mu$  cells; the cells show a gradation from the very thick walls of the outer layers to the thinner walls of the inner layers. The inner region is  $10-18 \mu$  wide and is formed of several layers of elongated thin-walled cells which are crushed as the asci mature.

The asci when young are cylindrical with a short flattened base and a rounded apex bearing a well-marked ring, they measure  $68-76 \times 6-9 \mu$  and have eight obliquely monostichous to subdistichous ascospores.

The ascospores are hyaline, oval, and often slightly flattened at each end, they become light brown, verrucose, and slightly constricted at the central septum, when mature they measure  $7.5-10 \times 4-5 \mu$ .

## CULTURES

On germination the ascospores produce one or more hyphal primordia from each cell of the spore and from any point of the wall. These hyphae soon branch and grow radially to form a superficial mycelium. Lateral phialides begin to develop in 3-5 days on the hyphae, these phialides are hyaline, subulate,  $20-45 \mu$  long and  $2-2.5 \mu$  at the base narrowing to  $0.75-1 \mu$  at the apex. One or more may arise from adjacent cells of the hyphae; hyaline, cylindrical to reniform conidia,  $3-6 \times 1.5-2 \mu$  are formed at the apex of the phialides where they remain in a mucilaginous globule.

In 7-10 days more complex conidiophores begin to develop; at first one or more phialides may be borne on a stalk cell but in later-formed conidiophores the stalk cell branches two or three times and each branch terminates in one or more phialides. These conidiophores are similar to those borne on the synnema which develop in cultures after about 14 days. These synnemata are formed of light brown hyphae which aggregate into ropes and grow upwards until they

are 300–500  $\mu$  long, many short lateral branches which surround the stalk of the synnema bear the phialides. The phialides are 22–45  $\mu$  long and 2.5–3.5  $\mu$  at the base, narrowing towards the apex where they terminate in a small cup. This cup

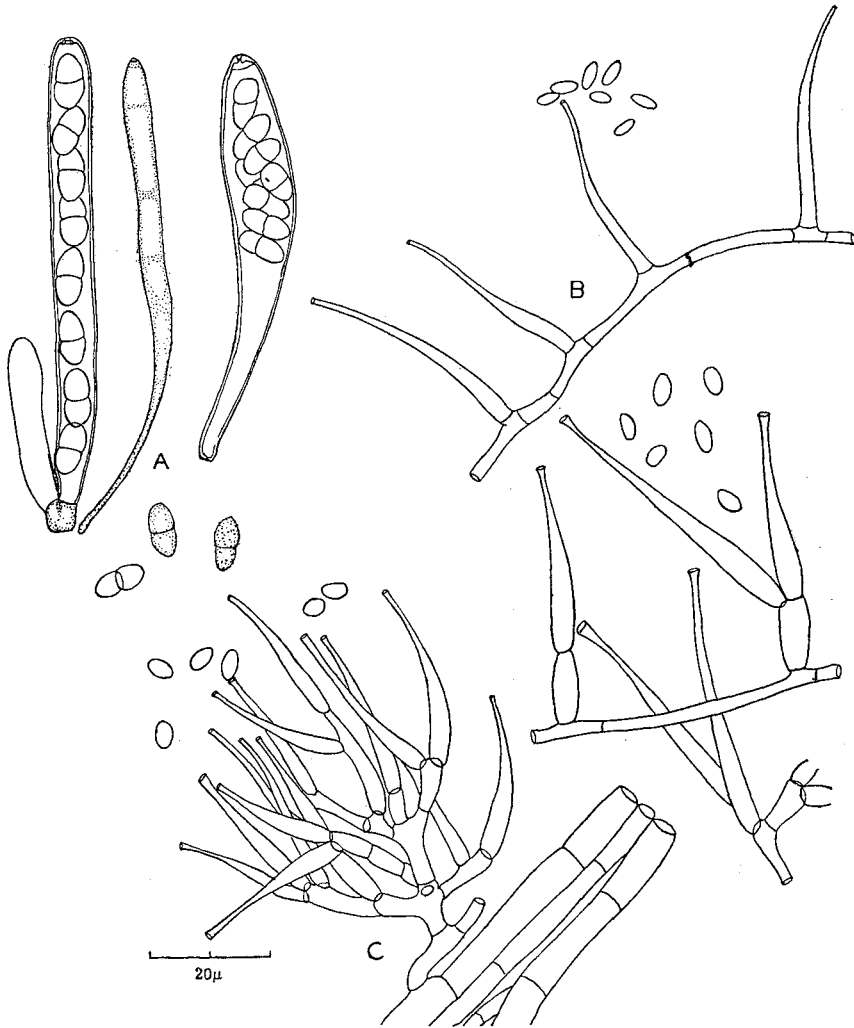


FIG. 29. *Nectria viridescens*. A, asci and ascospores; B–C, conidia and conidiophores from culture; B, 7-day cultures; C, part of synnema from 1-month old culture.

is formed by the first conidium to be produced, which arises endogenously in the closed tip of the phialide. As it develops, the tip is greatly stretched relative to its size so that when it finally ruptures to release the spore it remains for some time as an apical cup to the phialide.

The conidia produced from these phialides are pink in mass, globose, 4–5  $\times$  2–3  $\mu$  or may become reniform 6–8  $\times$  2.5–3  $\mu$ . They represent the secondary or macroconidia although they do not differ greatly from the microconidia in size or shape.

Cultures on 2 per cent. potato dextrose and on malt agar develop a deep green colour in the agar after 3–5 weeks. On potato dextrose agar the colony shows a marked zonation. The centre is deep green with a downy surface produced by the formation of masses of synnemata; this zone is surrounded by floccose mycelium with abundant conidiophores not on synnemata. The outer zone is formed of sparse aerial mycelium and shows a pale green discoloration of the agar.

## SPECIMENS EXAMINED

*Nectria viridescens* folder Herb. I.M.I.

On *Acer*, Howdale Woods, Yorks., W.G.B., June 58 (73617). On *Betula*, Cloughton Woods, Yorks., C.B., April 55 (59889); Gwydyr Forest, Llanrwst, Wales, C.B., May 58 (73377). On *Fagus*, Hardcastle Craggs, Yorks., R. Watling, April 57 (69125). On *Fraxinus*, Cloughton Woods, R. Watling, April 55 (59880). On *Pinus*, Cloughton Woods, Yorks., C.B., April 55 (59890). On *Salix*, Sawley Woods, Yorks., C.B., April 54 (56376).

*Nectria rishbethii* spec. nov.

This species was collected by Dr. Rishbeth on 10 September 1957 on the surface of a stump of Scots pine. This stump had been treated with 40 per cent. ammonium sulphate when the tree had been felled just over one year previously.

*Perithecia* flavide brunnea, ampulliformia, verrucosa, 150–250  $\mu$  dia. Stromata nulla.

*Asci* cylindraci, apice rotundati et cingulo refringenti porum circum ambienti praediti, octospori, 95–110  $\times$  9–11  $\mu$ .

*Ascosporae* ellipsoideae vel ovaes, 1-septatae, hyalinae vel pallide brunneae, leves, 8–12  $\times$  3.5–5  $\mu$ .

## In Cultura

*Mycelium* floccosum, album vel brunneum, ex hyphis ramosis, septatis, compositum, in agaro colorem fuscum efficiens.

*Conidiophora primaria* ramosa, phialides subulatas hyalinas, 23–35  $\mu$  longas, basi 2–3  $\mu$ , apice 1  $\mu$  latas, gerentia.

*Conidiophora secundaria* hyphis breviter ramosis sistencia ex synnematibus oriunda et phialides terminales efficientia.

*Phialides* obclavatae vel lageniformes, 10–16  $\times$  2.5–3  $\mu$ .

*Conidia* hyalina, globosa vel reniformia 2.5–4  $\times$  1–2  $\mu$ .

*Habitat* in ramis emortuis Pini sylvestris, Thetford Chase, prox. Thetford, J. Rishbeth, Herb. I.M.I. 70248b.

## DESCRIPTION

The perithecia are almost immersed in secreted resin, they are ampulliform with a short neck and rounded ostiolar papilla, the outer wall is rough, ochre to dresden brown in colour, and they measure 150–250  $\mu$  in diameter. Brown hyphae 3–4  $\mu$  wide arising from the base of the perithecium penetrate the host. In section the lateral wall of the perithecium is 26–34  $\mu$  wide and has an outer zone of 6–7 layers of thick-walled cells 10–12  $\times$  4  $\mu$ , or globose 3–6  $\mu$  in diameter,

these grade into thinner walled and more elongate cells in the inner layers. The inner zone is formed of 3-5 layers of very thin-walled hyaline cells which are crushed in the mature perithecium.

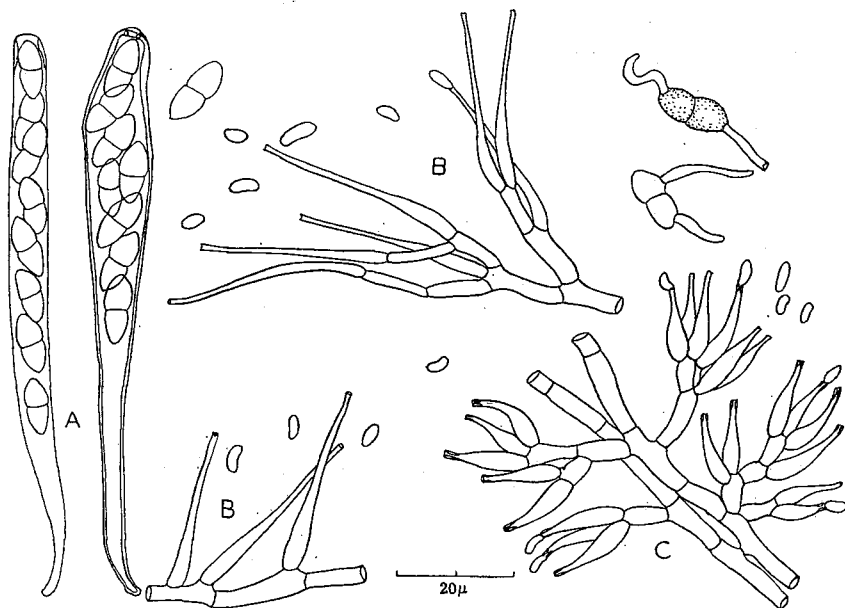


FIG. 30. *Nectria rishbethii*. A, asci and ascospores; B, primary conidiophores from 7-day old culture; C, secondary conidiophores which are borne on synnemata.

The asci are cylindrical with a rather flattened apex bearing a well-marked ring, they measure  $60-72 \times 6-7 \mu$  when the eight ascospores are obliquely monostichous but these become distichous before discharge when the asci measure  $95-110 \times 9-11 \mu$ .

The ascospores are ellipsoid to ovoid and slightly constricted at the single central septum. When young they are hyaline and smooth walled, but become light brown and often verrucose at maturity when they measure  $8-12 \times 3.5-5 \mu$ .

#### CULTURES

Ascospores were isolated on to malt and potato dextrose agar. On germination the ascospores form a hyphal primordium from each cell. These may arise from any point on the wall of the spore and give rise to a sparse colourless mycelium. The agar soon becomes light brown in colour and this darkens with age. Six week-old cultures begin to have a zonate appearance. Thus the point of inoculum is an erumpent mass of hyphae and surrounding this is a brown zone of developing synnemata. This brown zone is surrounded by a zone of sparse mycelium where conidia are formed from simple phialides on the prostrate hyphae. The outer zone is an area of floccose rapidly growing mycelium where spore formation is at a minimum. Cultures on malt agar show a stronger growth, the zones are not so distinct and the agar is brownish black.

Micro or primary conidia are developed in 2-3-day-old cultures from simple lateral phialides formed on the hyphae, these phialides are subulate  $25-35 \mu$

long and 2-3  $\mu$  at the base narrowing apically to 1-1.5  $\mu$ . These are followed in 5-7 days by branched conidiophores on which the branches terminate in phialides. In 3-4 weeks brown parallel hyphae grow upwards to form the stalks of the synnemata; several hyphae, each 4-5  $\mu$  wide, form the stalk and these have cells 20-44  $\mu$  long and 4-5  $\mu$  wide which show frequent anastomoses with adjacent cells. From these cells a brown substance is secreted which gives the stalk a slimy appearance. The conidiophores arise as tufts of shortly branched hyphae surrounding the conidiophores and each branch terminates in a tuft of phialides. These phialides are obclavate to lageniform 10-16  $\mu$  long and 2.5-3  $\mu$  at the base, narrowing to about 1  $\mu$  at the apex. Conidia formed from these phialides are oval to reniform, hyaline, 2.5-4  $\times$  1-2  $\mu$ . The discrete stromata formed at the point of the inoculum developed phialides over the surface and these produced conidia similar to those formed on the synnemata.

## SPECIMENS EXAMINED

*Nectria rishbethii* folder Herb. I.M.I.

On *Pinus sylvestris* stump treated with 40 per cent. ammonium chloride, Thetford Chase, near Thetford, J. Rishbeth, Sept. 57, Grid. ref. (Sheet 136 on 1") is 838887 (I.M.I. 70248b).

*Nectria brassicae* Ellis & Sacc., *Michelia*, ii, p. 374, 1881.

*Dialonectria brassicae* (Ellis & Sacc.) Cooke, *Grevillea*, xii, p. 110, 1884.

This description is based on the Co-type material distributed by Ellis, North Amer. Fung. No. 572 on *Brassica oleracea* and on the British collections made by Petch. No fresh material has been obtained and there is no evidence of the species having been grown. Petch left piles of *Brassica* stems in his garden and examined them periodically for the *Nectria*. I have found no other British records.

## DESCRIPTION

Perithecia scattered to gregarious on dead stems of *Brassica oleracea* and other herbaceous plants. They are globose with a conical ostiolar papilla and a smooth outer wall, on drying they show a lateral collapse involving the apex; they measure 100-150  $\mu$  in diameter. In section the lateral wall is 15-22  $\mu$  wide and formed of 4-5 layers of rather large cells 6-16  $\times$  4-6  $\mu$ , which show a gradation from the thick-walled cells of the outer 2-3 layers to the thin-walled cells of the inner layers. There are 3-4 layers of very thin-walled hyaline cells lining the perithecial cavity but these are almost obscured in mature perithecia.

The asci are cylindrical to clavate with a short truncate base and a rounded apex bearing a central pore, they measure 40-65  $\times$  7.5-14  $\mu$  and have eight obliquely monostichous to distichous ascospores.

The ascospores are ellipsoid to cylindrical with a rather larger upper cell and measure 10-16  $\times$  4-5  $\mu$ . They become light brown when mature.

The perithecia are associated with pionnotes 150-250  $\mu$  in diameter which are covered with *Fusarium* macroconidia. These macroconidia are lunate with an

acute apex and elongated *Fusarium* foot cell, they have 4-6 transverse septa and when mature measure  $40-45 \times 4-4.5 \mu$ . These are presumed to be the conidial state as they show a close relationship with the macroconidia of most other members of this group. However, the species has not been grown.

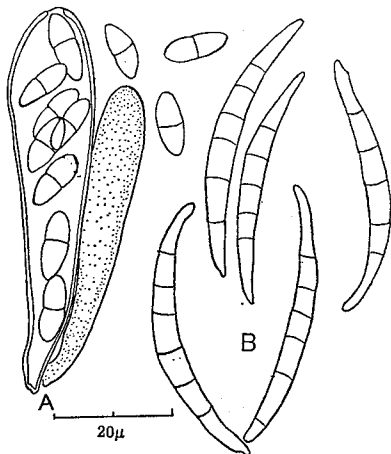


FIG. 31. *Nectria brassicae*. A, asci and ascospores; B, associated conidia on host.

#### SPECIMENS EXAMINED

*Nectria brassicae* folder Herb. R.B.G. Kew

Ellis, North Amer. Fung. 572 (1881), *Nectria brassicae* on old stems of *Brassica oleracea*, July 1880. (This is taken as authentic material as it agrees with the description in Michelia and was cited by Ellis & Ev.) Ellis, N.A.F. 572b (2-parts) on *Solanum tuberosum*, Newfield, N.J., Sept. 1883; Ex. Libert, 790 *Nectria brassicae*.

*Nectria brassicae* folder Herb. B.M. Nat. Hist.

*Nectria brassicae* on *Brassica*, North Wootton, T. Petch (3-collections), Oct. and Nov. 35; Mar. 42.

#### THE PEZIZA GROUP

Only one representative of this group has been recorded for Britain, namely, *Nectria peziza*. It is characterized by the subglobose non-stromatic yellow-brown perithecia which undergo a cupulate collapse when dry. The wall has two regions, the outer, which forms the greater part of the wall, is formed of thin-walled almost delicate polyhedral to globose cells whilst the inner layer is formed of compressed elongate cells.

*Nectria peziza* (Tode ex Fr.) Fr., Summ. Veg. Scand. ii, p. 388, 1849.

*Sphaeria peziza* Tode, Fung. Meckl. ii, p. 46, 1791.

*Sphaeria peziza* Tode ex Fr., Syst. Myc. ii, p. 452, 1823.

*Nectria aurea* Cooke, *Grevillea*, viii, p. 9, 1879.

*Nectria epigaea* Cooke, *Grevillea*, viii, p. 10, 1879.

*Dialonectria aurea* (Cooke) Cooke, *Grevillea*, xii, p. 110, 1884.

*Byssonectria epigaea* (Cooke) Cooke, *Grevillea*, xii, p. 109, 1884.

*Dialonectria peziza* (Tode ex Fr.) Cooke, *Grevillea*, xii, p. 110, 1884.

*Neuronectria peziza* (Tode ex Fr.) Munk, *Dansk bot. Ark.*, xvii, p. 58, 1957.

Munk (1957) took *Nectria peziza* as the type species of his genus *Neuronectria*. This he distinguished from *Nectria* by the thin-walled cells of the outer perithecial wall, by the lack of paraphyses, the obclavate asci, and the presence of longitudinal ridges on the epispore of the ascospore.

The perithecial wall of *Nectria peziza* shows no greater divergence from *N. cinnabarina* than do any of the *Nectrias* in the *Mammoidea* or *Sinopica* groups. In all *Nectria* species where the asci cover the whole of the inner perithecial wall below the paraphyses, there is a tendency for them to be obclavate due to the central compression, but I find the asci in *N. peziza* to be predominately cylindrical. With regard to the ascospores, similar longitudinal ridges occur on the ascospores of *N. haematococca* and *N. arenula*. This character occurs sporadically throughout the Ascomycetes and the Sphaeropsidales and can only be regarded as of specific importance.

#### DESCRIPTION

The perithecia, which are superficial and without a stroma, may be seated on, or associated with, a sparse byssus; they are pale yellow when young but later become orange to almost brown. Mature perithecia tend to undergo a cupulate collapse when dry or after spore discharge. Under the hand lens the outer wall appears crystalline, slightly roughened, with a small central ostiolar papilla darker than the rest of the wall; they measure 250–360  $\mu$  in diameter. In section the lateral wall is 50–65  $\mu$  wide and shows a differentiation into two distinct regions. The outer is 35–45  $\mu$  and formed of thin-walled oval to globose cells 20  $\times$  10  $\mu$  or 8–14  $\mu$  in diameter. The inner region is 14–18  $\mu$  wide and formed of elongate compressed cells 10  $\times$  2  $\mu$ ; these cells have denser contents and give the wall its colour.

The asci cover the whole of the inner perithecial wall below the paraphyses, they are cylindrical, occasionally obclavate, with a rounded undifferentiated apex in the mature asci. In young asci a central canal is visible through a gelatinous apical plug, the ascospores form below this, but the plug dissolves before they are mature. The asci measure 75–90  $\times$  8–10  $\mu$  and the obliquely monostichous ascospores may become distichous before discharge.

The ascospores are hyaline, ellipsoid, with a single central septum; when mature, longitudinal striations are present on the outer spore wall which turns straw-coloured; they measure 12–15  $\times$  5–7  $\mu$ .

#### CULTURES

The first cultures of this species were obtained from a collection of perithecia on *Polyporus squamosus* on elm (I.M.I. 53559). The ascospores grew readily and several single ascospores were isolated on to maize-meal agar and malt agar. After 7 days the surface of the agar was covered with a sparse growth of hyaline mycelium and a slight brown discoloration of the agar had occurred. Simple



lateral phialides developed, often from adjacent cells of the same hyphae, these phialides are simple subulate,  $40-60\mu$  long and  $3\mu$  at the base, narrowing to  $1.5\mu$  at the apex where the lateral wall is thickened to form a collar. Conidia formed endogenously at the base of the collar are hyaline, cylindrical to ellipsoid, and measure  $5-8 \times 2.5-3.5\mu$  in diameter.



FIG. 32. *Nectria peziza*. A, asci and ascospores; B, conidia and phialides from 7-day old culture; C, conidia and phialides from 1-month old culture.

In cultures, about 3 months old, shorter broader phialides develop on branched conidiophores, they measure  $15-20 \times 3-4\mu$ . Conidia formed from these are  $8-11 \times 3-4\mu$  and may represent the macroconidia.

Perithecial formation in culture is effected by light. None formed in cultures kept in the dark, whereas they formed on a variety of media in cultures kept in the light and most profusely on maize-meal agar.

#### *Habitat*

Common on moist and decayed wood and on decayed *Polyporus* spp., less frequent on bark, soil, and old cloth.

#### SPECIMENS EXAMINED

Authentic exsiccata

Fries, Scler. Suec. xxiv, No. 235 (1822) *Sphaeria peziza* Herb. R.B.G. Edinburgh (collections in Herb. R.B.G. Kew in poor condition).

*Nectria peziza* folder Herb. R.B.G. Kew

British exsiccata

Berk., British Fungi, iii (1837), 176 *Sphaeria peziza*. (All the rest as *Nectria peziza*.) Thümen, Myc. Univ. vii (1877) 654; Plowr., Sphaer. Brit. ii (1875) 7; ibid. iii (1878) 7; Thümen, Myc. Univ. xxii (1883) 2165 v ar. *fungicola*; Roum. Fungi Sel. Exs. xlvi (1889) 4759 var. *fungicola*.

Other exsiccata

As *Nectria peziza*. Fuckel, Fung. Rhen. x (1864) 982; Karsten, Fungi Fenn. x (1870) 994; Thümen, Fungi Austr. xiii (1874) 1262; Sydow, Myc. Mar. vii (1884) 662.

*Nectria rimicola* folder Herb. R.B.G. Kew

*Nectria (Dialonectria) rimicola* on stump, Queens Cottage, Kew (Cooke), July 88. (The type material of this species is on the same sheet but is without perithecia.)

*Nectria aurea* folder Herb. R.B.G. Kew

On *Polyporus squamosus*, Kew (scripsit Cooke). On *Polystictus*, York, Masee 10.9.09 (scripsit Cooke).

*Nectria epigaea* folder Herb. R.B.G. Kew

On ground, Penecuk, N.B., 1878.

*Nectria peziza* folder Herb. R.B.G. Edinburgh

Cooke, Fungi Brit. exs. ed. 2, vi (1875-9) 563 *Nectria peziza*. Sydow, Myc. Germ. viii (1905) 388, *Nectria peziza*. Petrak, Flora Bohem. et Morav. exs. 2, ii (?1914) 74, *N. peziza*.

*Nectria peziza* folder Herb. I.M.I.

On *Acer*, Leighton Buzzard, Beds., D. A. Reid, Nov. 55 (61362). On *Betula*, Esher, Surrey, S. P. Wiltshire, Aug. 54 (57757). On Elm, Sudbury, Suffolk, R. Gooden, Nov. 53 (53869). On *Fagus*, Henley, Oxon., J.E., Nov. 33 (52162); Denmark, R. W. G. Dennis, Oct. 55 (61237); Berkhamsted, Herts., A. H. S. Brown, Oct. 55 (61243a). On *Malus*, Stibbington, Hunts., D. A. Reid, Sept. 56 (63745). On *Polyporus squamosus*, Mulgrave Woods, Yorks., C.B., Sept. 53 (53559).

*Incorrectly named exsiccati issued as Nectria peziza*

Moug. & Nestl., Stirp. cryp. Vog. Rhen. v (1815) 483 *Sphaeria peziza* = *Nectria veuillotiana* (parts examined from Kew, I.M.I., and Edinburgh).

Desm., Pl. crypt. France ed. 1, ser. 1 (1825) 35 *Sphaeria peziza* = *Nectria coccinea* (Kew).

Rav., Fungi Amer. exs. vii (1882) 647 *Nectria peziza* = *Nectria* of the 'sanguinea' group on *Parodiopsis perisporioides* on leaves (Kew and Edinburgh).

Libert, Herb. Jard. Bot., Bruxelles, No. suppl. 732 *Sph. peziza* Auctor non Tode = *Nectria veuillotiana* (Kew).

#### THE ARENULA GROUP

The perithecia are yellow to brown and seated upon a thin discrete stroma or byssus. In section, the wall has an outer region of thin-walled globose cells and an inner region of thicker-walled oval and somewhat compressed cells. The

ascospores are fusoid to ellipsoid with faint longitudinal striations on the outer ascospore wall when mature.

*Nectria arenula* is the only British species of this group, which is allied to *N. coprosmae* Dingley, described from New Zealand. No fresh material of *N. arenula* has been obtained, but Miss Dingley (1957) says that *N. coprosmae* produces *Fusarium*-like conidia on pionnotes.

In the solitary collapsed perithecia which have large thin-walled cells in the outer layers, and in the longitudinal striations of the ascospores, *Nectria arenula* shows certain affinities with *N. peziza*.

***Nectria arenula*** (Berk. & Br.) Berk., Outl. Brit. Fung., p. 394, 1860.

*Sphaeria arenula* Berk. & Br., *Ann. & Mag. nat. Hist.*, 2, ix, p. 320, 1852.

*Dialonectria arenula* (Berk. & Br.) Cooke, *Grevillea*, xii, p. 110, 1884.

*Nectria bloxami* Berk. & Br., *Ann. & Mag. nat. Hist.*, 2, xiii, p. 467, 1854.

*Calonectria bloxami* (Berk. & Br.) Sacc., *Atti Soc. Ven. Padova*, iv, pp. 101-141 (separate p. 23), 1875.

*Nectriella bloxami* (Berk. & Br.) Fuckel, *Symb. Myc., Nachtr.*, iii, p. 21, 1877.

*Dialonectria bloxami* (Berk. & Br.) Cooke, *Grevillea*, xii, p. 100, 1884.

*Nectria arenula* grows on herbaceous stems and has scattered yellowish-brown perithecia. The only material of *N. graminicola* available for study in Britain shows a close affinity with this species, but the material is too fragmentary for the name to be considered, with any certainty, as a synonym of this species. *N. graminicola* is further discussed under this name.

#### DESCRIPTION

The perithecia are scattered, yellow to yellow-brown with a smooth to verrucose outer wall. They show a pomiform to cupulate collapse when dry with an

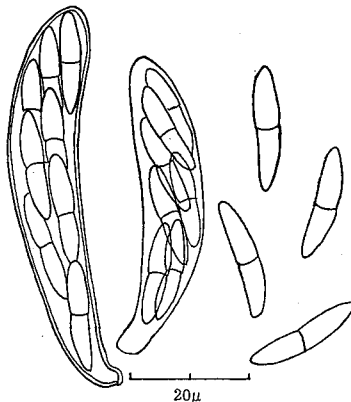


FIG. 33. *Nectria arenula*. Asci and ascospores.

upright central ostiolar papilla and measure 180-250  $\mu$  in diameter. In section, the lateral wall is 20-26  $\mu$  wide and formed of two regions. The outer is 10-16  $\mu$  wide and formed of hyaline thin-walled, globose cells, 10-12  $\times$  5-8  $\mu$ . The inner layer is formed of smaller and rather thicker-walled, oval to hexagonal cells, 3-8  $\times$  2-3  $\mu$ .

A thin stroma which forms a cushion below the perithecia is formed of hyaline hyphae 3–4  $\mu$  wide which both penetrates the epidermis of the host and spreads out radially on the surface.

The asci are clavate with a short truncate base and a rounded apex bearing a pore. They measure 45–60  $\times$  8–10  $\mu$  and have eight distichous ascospores.

The ascospores are fusoid to ellipsoid and occasionally slightly curved, they are hyaline with faint longitudinal striations when mature and measure 15–18  $\times$  3.5–4  $\mu$ .

#### SPECIMENS EXAMINED

*Nectria arenula* folder Herb. R.B.G. Kew

167 *Sphaeria arenula* B. & Br. on *Aira caespitosa*, St. Catherines (Batheaston) 22 Feb. 1851 (Co-type, ex Herb. Berk.). There are six other parts ex. Herb. Berk., Cooke, Currey and Leighton which are all parts of the same collection.

*Nectria bloxami* folder Herb. R.B.G. Kew

*Sph.* (*Nectria*) on Jerusalem artichokes, Twycross (with letter dated 16 Nov. 1855). This is taken to be the type collection. Other specimens ex Herb. Berk., Cooke and Currey are presumably parts of the same collection. On *Heraclium*, Ex Herb. Currey.

*Nectria arenula* folder Herb. I.M.I.

On *Carex*, Surlingham Broad, Norfolk, E.A.E., Sept. 44 (75355); Wheatfen Broad, Norfolk, E.A.E., Oct. 44 (75358). On *Glyceria*, Brundall, Norfolk, E.A.E., Oct. 45 (75356). On *Typha*, Surlingham Broad, Norfolk, E.A.E., Sept. 44 (75357).

#### THE LASIONECTRIA GROUP

*Lasionectria* was proposed by Saccardo (1883) as a subgenus of *Nectria* for species with 'minutely pilose perithecia'. It was raised to generic rank by Cooke (1884) and retained by Petch (1938). However, as the presence of hairs on the outer perithecial wall is the sole character separating the genus from *Nectria* it can only be considered as of poor generic status and in my opinion is best considered as a subdivision of the genus.

This group is represented in Britain by four species: *Nectria ellisii*, *N. lecanodes*, *N. funicola*, and *N. aureola*.

These four British species have subglobose perithecia which are sessile or seated on a thin byssus. They have a uniform perithecial wall structure of small oblong cells which have progressively thinner walls towards the central layers. The asci are clavate with distichous ascospores, and have an undifferentiated apex in *N. lecanodes* and *N. funicola* but *N. ellisii* has an apical ring.

*Nectria leptosphaeriae*, placed in this genus by Petch, does not have true perithecial hairs and in this paper the species is described in the *Episphaeria* group. The only species of the 'Lasionectria' group to be grown is *N. ellisii*, in this species the conidial production is sparse and the cylindrical conidia are predominately aseptate but may become 1-septate.

## KEY TO SPECIES

Perithecia developing on herbaceous plant material . . . . .	<i>N. ellisii</i>
Perithecia developing in association with lichens . . . . .	<i>N. lecanodes</i>
Perithecia developing on cardboard, rope, &c. . . . .	<i>N. funicola</i>
Perithecia as hyperparasites on <i>Meliola</i> on <i>Rhododendron</i> . . . . .	<i>N. aureola</i>

***Nectria ellisii* spec. nov.**

This is the species for which the name *Nectria flavida* Corda (*Lasionectria flavida*) has been used in Britain. The name was first used for a British collection by Broome on bramble, Leighwood, Bristol, Dec. 1847. This was provisional,

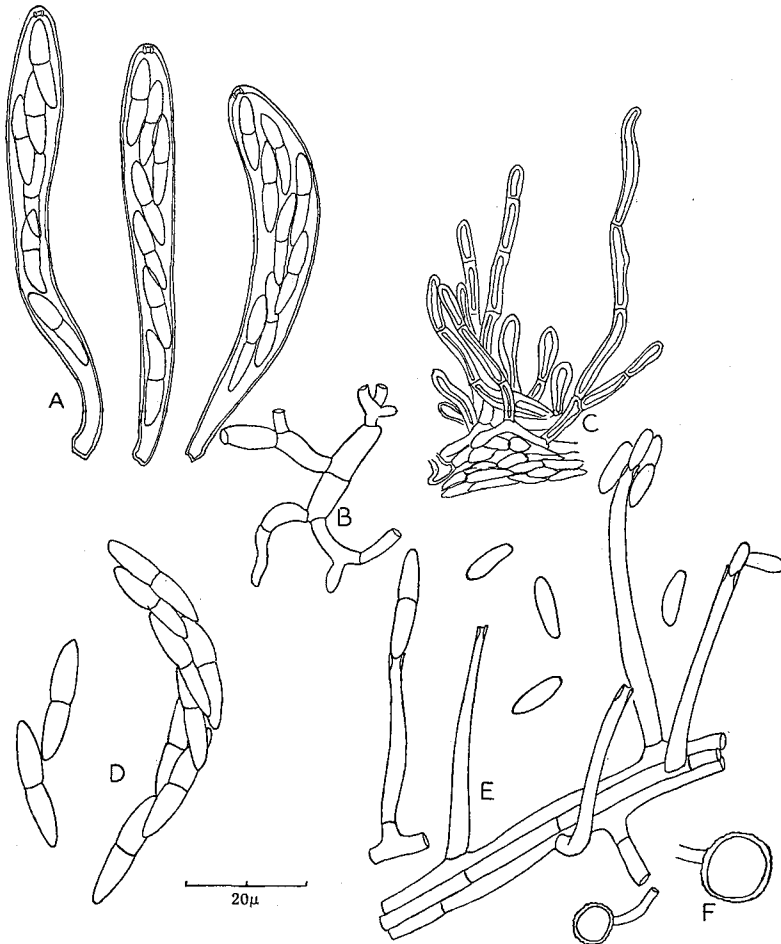


FIG. 34. *Nectria ellisii*. A, asci and ascospores; B, germinating ascospore; C, hairs on outer perithecial wall; D, ascospores of *N. graminicola*; E, conidiophores and conidia of *N. ellisii* formed in culture.

for a note by Broome states, 'This has not been compared with authentic material'. The species was transferred to *Lasionectria* by Cooke (1884).

To my knowledge there is no Corda material of this species in existence. The British collections of *Nectria ellisii* cited, including those mentioned by Broome,

differ from Corda's description and figures of *N. flavida*. The latter was figured by Corda as possessing a pronounced beak. *N. ellisii* has no beak whatever, it also differs in the shape of the asci and ascospores and in the host. *N. flavida* was described as occurring on *Alnus glutinosa*, whereas *N. ellisii* is predominantly on herbaceous hosts.

*Perithecia* dispersa, globosa, flavida per porum apicalem aperta, 140–160  $\mu$  alta, 120–160  $\mu$  dia., setis hyalinis ramosis 30–70  $\times$  2–4  $\mu$  vestita; paries perithecialis 13–20  $\mu$  crassus.

*Asci* cylindrici, basi truncati, subsessiles, apice rotundati et cingulo refringenti porum circumambienti praediti, octospori, 35–55  $\times$  6–8  $\mu$ .

*Ascosporae* distichae, hyalinae, fusoidae, 1-septatae, 11–12  $\times$  3–5  $\mu$ .

*Conidiophora* (seu phialides simplices) hyalina, aliquoties e cellula basali oriunda, 35–50  $\times$  2.5–3  $\mu$ .

*Conidia* cylindrica, apice rotunda, continua vel 1-septata, 4–12  $\times$  2–2.5  $\mu$ .

*Chlamydosporae* globosae 9–10  $\mu$  dia., tunica 1.5–2  $\mu$  crassa, verrucosa, praeditae.

*Hab.*, in foliis emortuis *Phragmitis communis*, Surlingham Broad, Norfolk, E. A. Ellis, Sept. 1955 (I.M.I. 60998).

#### DESCRIPTION

The perithecia are scattered to gregarious, superficial and without a stroma, on the stems of herbaceous plants. They are globose 120–160  $\mu$  in diameter and 140–160  $\mu$  high, and yellow in colour. The outer wall is covered with white branched hairs up to 70  $\mu$  long and 2–4  $\mu$  wide at the base narrowing slightly towards the rounded apex. The lower branches form a mesh over the perithecial wall. In section, the lateral wall is 13–20  $\mu$  wide and composed of two regions. The outer, 9–16  $\mu$  wide, is composed of 5–6 layers of elongated cells, with thick walls in the outer layers, these become progressively thinner towards the inner layers. The inner region is 4–6  $\mu$  wide and formed of very thin-walled compressed cells.

The asci are cylindrical with a short flattened base and a rounded to flattened apex containing a central pore; they measure 35–55  $\times$  6–8  $\mu$  and have eight distichous ascospores. The asci cover the whole of the interior perithecial wall. Those below the periphysis are almost horizontal and shorter than those arising from the base.

The ascospores are hyaline, fusoid, straight or slightly curved, and 11–12  $\times$  3–4  $\mu$ .

#### CULTURES

Ascospores germinated readily but growth was slow, at 22° C. it extended only 3 cm. along the agar slope after 4 weeks. The aerial mycelium was floccose, cottony, with a yellow discoloration of the media. The surface of the agar slope was covered with mycelium after 8–10 weeks and by this time the agar had developed a yellow to orange discoloration.

Conidiophore production was initially very poor, the first *Cephalosporium*-like conidiophores were found after 20 days. These phialides are 35–50  $\mu$  long and 2.5–3  $\mu$  at the base, they narrow slightly towards the apex where the lateral wall

is thickened slightly to form a collar. Conidia formed from these phialides are cylindrical with rounded ends and may become 1-septate, they measure  $4-7 \times 2-2.5 \mu$  or up to  $12 \mu$  long when 1-septate.

Chlamydospores developed as intercalary or terminal swellings of the hyphae in 4-5 weeks. They are  $9-10 \mu$  in diameter with a roughened outer wall  $1.5-2 \mu$  thick.

## SPECIMENS EXAMINED

*Calonectria flavida* folder Herb. R.B.G. Kew

On ?Bramble, *Sphaeria flavida*, Leighwood, Bristol, No. 387, Dec. 1847 (Ex Herb. Broome). *Sphaeria (Nectria) flavida*, Nightingale Valley, Dec. 1847; Bath-easton, Mar. 1869.

*Nectria ellisii* folder Herb. I.M.I.

On *Epilobium*, Wheatfen Broad, Norfolk, E.A.E., May 57 (69362c). On *Eupatorium*, Wheatfen Broad, Norfolk, E.A.E., May 50 (41596). On *Filipendula*, Wheatfen Broad, Norfolk, M.B.E., Oct. 58 (75248). On *Lychnis*, Bec. du Nez, Guernsey, M. B. and J. P. Ellis, Sept. 48 (34411). On *Phragmites*, Surlingham Broad, Norfolk, E.A.E., Sept. 55 (60998).

✓  
***Nectria lecanodes*** Cesati in Rabenh., Herb. Myc., ed. 2, vi, No. 525, 1857, sub.

*Sphaeria (Nectria) lecanodes*.

*Lasionectria lecanodes* (Ces.) Petch *Trans. Brit. mycol. Soc.*, xxi, p. 267, 1938.

*Nectria peziza* var. *minor* Desm., *Bull. Soc. bot. Fr.*, iv, p. 997, 1857.

*Dialonectria lecanodes* (Ces.) Cooke, *Grevillea*, xii, p. 110, 1884.

This species occurs only on lichens, most frequently on *Peltigera canina*. Wollenweber, who examined Sydow's Myc. Germ. Exs. 247 *Nectria lecanodes*, considered it to be a synonym of *N. bulbicola* P. Henn. In this exsiccatum, many of the perithecia are over-mature and have lost the hairs from the outer wall.

## DESCRIPTION

Perithecia are superficial and seated on a thin byssoid stroma which becomes intermingled with and indistinguishable from the host tissue. They are pale yellow to orange in colour with the outer wall covered with white hairs. When young, they are globose, but show a pomiform to almost cupulate collapse when mature. They measure  $130-200 \mu$  in diameter.

In section, the lateral wall is  $15-20 \mu$  wide and formed of 7-10 layers of elongated cells  $10-12 \times 2.5-3 \mu$ ; these cells have progressively thinner walls from the outer to inner layers. The cells of the outer layer form the superficial hairs that cover the outer perithecial wall, these are hyaline, undulate  $2-3 \mu$  wide, and usually about  $30 \mu$  long.

The asci are clavate with a thin undifferentiated apex and eight distichous ascospores, they measure  $50-65 \times 6-8 \mu$ .

The ascospores are hyaline, ellipsoid, and slightly constricted at the septum, when mature they become light brown and verrucose and measure  $9-12 \times 3-4 \mu$ .

## SPECIMENS EXAMINED

*Nectria lecanodes* folder Herb. R.B.G. Kew

Raben., Herb. Myc. ed. 2, vi. 525 (1857) (authentic name for *Nectria lecanodes*). Fuckel, Fung. Rhen., 2050 (1867). Rehm, Ascomycen 38 (1870). Plowr. Sphaer. Brit. xi. 212 (1875) and cxi. 12 (1878). Cooke, Fungi Brit. Exs. ed. 2, vi. 564 (1875-79). Roum., Fungi Gall. Exs. vii. 665 (1880). Thümen, Myc. Univ. xviii. 1746 (1881). Sydow, Myc. March. iv. 346 (1882). Arnold, Lich. Exs. 1672 (1894-99). Sydow, Myc. Germ. v. 247 (1904). Jaap, Fungi Sel. Exs. xv. 371a and 371b (1909).

*Nectria peziza* folder Herb. R.B.G. Kew

Desm., Pl. Crypt. Fr. ed. 2, viii. 371, *N. peziza* var. *minor* Desm.

*Nectria funicola* (Berk. & Br.) Berk., Outl. Brit. Fung., p. 393, 1860.

*Lasionectria funicola* (Berk. & Br.) Cooke, *Grevillea*, xii, p. 112, 1884.

*Sphaeria funicola* Berk. & Br., *Ann. & Mag. nat. Hist.*, Ser. 2, vii, p. 188, 1851.

*Nectria chartaecola* Fuckel, Fungi Rhen. Exs., x, No. 990, 1864.

*Nectriella charticola* Fuckel, Symb. Myc., p. 176, 1870.

*Nectria charticola* (Fuckel) Sacc., *Michelia*, 1, p. 289, 1878.

*Calonectria funicola* (Berk. & Br.) Sacc., *Michelia*, 1, p. 312, 1878.

*Nectriella funicola* (Berk. & Br.) Petch, *Naturalist*, Lond., p. 281, 1937.

## DESCRIPTION

This species was described from a collection of perithecia growing over the strands of jute in a decaying rope. The perithecia are scattered to gregarious and often seated on a thin stroma, they are yellow to orange in colour and obpyriform in shape owing to the prominent beak and measure 125-190  $\mu$  in diameter. The outer perithecial wall is covered with sparse white hairs 40-55  $\mu$  long and 4  $\mu$  at the base, they narrow somewhat towards the apex which is encrusted with a white crystalline substance.

In section, the lateral wall is 25-32  $\mu$  wide and formed of 6-8 layers of elongated cells 9-12  $\times$  3-4  $\mu$ . The cells in the outer layers have thick walls but the walls become progressively thinner towards the inner layers.

The asci are clavate with a thin wall undifferentiated at the apex, they have eight distichous ascospores and measure 70-95  $\times$  12-17  $\mu$ .

The ascospores are ellipsoid to ovoid and slightly constricted at the septum, they are hyaline with a smooth wall and measure 16-20  $\times$  6-8  $\mu$ .

This species occurs on decaying rope, cardboard, and paper, but has been infrequently collected.

## SPECIMENS EXAMINED

*Calonectria funicola* folder Herb. R.B.G. Kew

*Sph. funicola* B. & Br., Kings Cliffe, Oct. 22, 1841 (Type Coll.).

*Nectria charticola* folder Herb. R.B.G. Kew

Fuckel's Fung. Rhen. 990 *Nectria chartaecola* Fuckel.



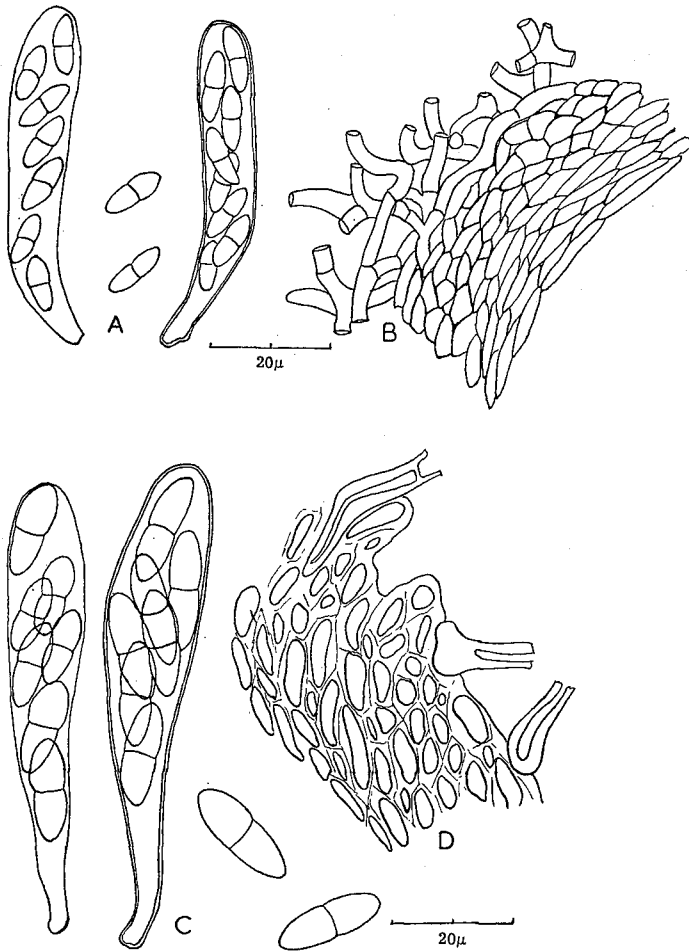


FIG. 35. *Nectria lecanodes*. A, asci and ascospores; B, part of lateral perithecial wall.  
*Nectria funicola*. C, asci and ascospores; D, part of lateral perithecial wall.

*Nectria aureola* Winter, *Hedwigia*, xxiv, p. 261, 1885.

*Lasionectria aureola* (Winter) Petch, *Trans. Brit. mycol. Soc.*, xxi, p. 267, 1938.

*Nectriella aureola* (Winter) Höhnelt (in error), *S.B. Akad. Wiss. Wien*, I, cxviii, p. 820, 1909.

When Höhnelt was discussing Nectriaceae on *Meliola* sp. he inadvertently listed *Nectria aureola* Winter as *Nectriella*.

The British records of this species are based on a collection by Boyd in 1907 and this is the only collection seen by me. In fact, this is probably the only collection since the one described by Winter. As the few remaining perithecia on Boyd's collection were not mounted, I have nothing to add to the original description by Winter. This was also cited by Petch (1938) and Hansford (1946). The latter stated that it closely resembled *Calonectria limpida*.

## DESCRIPTION

Perithecia gregarious, short conoid to globose, with short, rigid, simple, obtuse setae on the upper part, pale golden-yellow, transparent. Asci oblong, fusoid, shortly stipitate, 8-spored,  $47-53 \times 7 \mu$ . Spores fusoid, slightly attenuate to the sharply pointed ends, 1-septate not constricted,  $14 \times 2.5 \mu$ , hyaline.

## SPECIMENS EXAMINED

*Nectria aureola* folder Herb. B.M. Nat. Hist.

On *Meliola niessleana* on *Rhododendron*, Killin, Perth, Scotland, D. A. Boyd, July, 07.

## INCOMPLETELY KNOWN OR MISDETERMINED BRITISH NECTRIAS

*Nectria caulina* Cooke, *Grevillea*, v, p. 62, 1876.

The type material of this species in Herb. Kew is a *Ditopella*, probably *D. vizeana* Sacc. Cooke presumably considered this to be a cauline form of *Hyponectria buxi*.

*Nectria citrino-aurantia* de Lacr. in Desm., Pl. Crypt. Fr., ser. 2, Fasc. xvi, No. 778, 1860.

*Calonectria citrino-aurantia* (de Lacr.) Sacc., *Michelia*, I, p. 314, 1878.

The British records of this species are based on collections by Broome from Batheaston, 1873 and 1874. The only other British collection seen by me is in the British Museum as immature *Nectria ochroleuca*.

Sections of the co-type material show the perithecia to be partially embedded in a stroma, this may indicate that they were somewhat immature, or, on the other hand, that the species should be assigned to the genus *Hypocreopsis* Karsten.

The superficial appearance of the yellow perithecia on a stroma suggest the *Ochroleuca* group, but from the material available for examination it cannot be placed here with any confidence.

## DESCRIPTION

The minute perithecia develop just below the surface of the stroma. This is 1-1.5 mm. in diameter and arises in the cortex of the host. It has a homogeneous structure and is formed of pseudoparenchymatous tissue with small cells.

The perithecia are densely crowded, ovoid with a smooth yellow and semi-transparent wall, they measure 80-120  $\mu$  in diameter. The surface of the stroma is covered by the perithecia and they appear gelatinous when moistened. In section the lateral wall is 18-22  $\mu$  wide and formed of three regions. The outer is 6-8  $\mu$  wide and consists of 3-4 layers of gelatinous cells. The central region is 7-10  $\mu$  wide and formed of 3-4 layers of thick-walled oval to globose cells  $3 \times 2 \mu$ . The inner region is formed of thin-walled cells which appear somewhat gelatinous.

The asci are clavate with a thin rounded apex and eight obliquely monostichous to distichous ascospores, they measure  $30-38 \times 5 \mu$ .

The ascospores are cylindrical with rounded ends, hyaline and become constricted at the central septum, they measure  $7-8 \times 2.5-3 \mu$ .

No associated conidial state was found on the collections examined.

## SPECIMENS EXAMINED

*Nectria citrino-aurantia* folder Herb. R.B.G. Kew

Desmazières, Crypt. Fr. ser. ii, 778 (1860); also in Rabenhorst, Fung. europ., 325 (1861) (both Co-type material). On (?) *Salix*, Batheaston, C. E. Broome 1873 (ex Herb. Currey).

*Nectria citrino-aurantia* folder Herb. B.M. Nat. Hist.

On willow (*Salix*), Batheaston, Dec. 63 (? 73) Broome (ex Herb. Plowright).  
On rotten sticks, Batheaston, Dec. 1873, No. 398.

*Nectria ochroleuca* folder Herb. B.M. Nat. Hist.

On bark, Selby Oak, Dec. 09 (as immature *Nectria ochroleuca*).

*Nectria furfurella* Berk. & Br., *Ann. & Mag. nat. Hist.*, ser. 4, vii, p. 435, 1871.

Petch (1938) transferred this species to *Pseudonectria*. No perithecia are left on the type collection and no further collections agreeing with Berkeley and Broome's description have been found.

*Nectria fuscospora* Plowright in Atkinson, *The Westmorland Note Book and Natural History Record*, p. 90, 1888.

*Letendraea fuscospora* (Plowr.) Petch, *Naturalist*, Lond., 822, p. 94, 1947.

This species was collected on an old shoe at Bowness. I have been unable to find any type material of this species in the British Herbaria. A collection in the British Museum labelled *Letendraea fuscospora* (Plowr.) Petch on a stump of *Pinus sylvestris* is *Nectria viridescens*. There is little evidence to show that this is the same species as Atkinson's collection on the old shoe, and I think that there is little justification for using the name *N. fuscospora* as an earlier name for *N. viridescens*. Until further collections are obtained, *N. fuscospora* must be considered as a nomen dubium.

*Nectria graminicola* Berk. & Br., *Ann. & Mag. nat. Hist.*, 3, Ser. iii, p. 376, 1859.

*Nectriella graminicola* (Berk. & Br.) Niessl in Rabenh., Fung. Eur. Exs. xvii. No. 1652, 1873.

*Dialonectria graminicola* (Berk. & Br.) Cooke, *Grevillea*, xii, p. 110, 1884.

There are three collections in the type folder in Herb. R.B.G. Kew, and one in the British Museum. On all this material the perithecia are sparse. Those that remain resemble *Nectria arenula* and have similar 1-septate ascospores that measure  $16-19 \times 3-4 \mu$ .

Ihssen (1910) stated that *Nectria graminicola* is the perithecial state of *Fusarium nivale*, the snow mould of grasses and cereals. Ihssen identified his species from Winters' description in Rabenhorst, Krypt. Fl. 1, 2, p. 120, 1887. Weese (1913) stated that Ihssen's statement was probably incorrect as Ihssen's perithecial material which he examined was either a *Leptosphaeria* or a *Meta-sphaeria*.

Wollenweber (1913) agreed with Ihssen. He found that his isolations, started

from conidia, developed perithecia which he believed to be the same species as Berkeley and Broome's, and he transferred it to *Calonectria graminicola* (Berk. & Br.) Wollenweber.

The question we are concerned with here is whether or not *Calonectria graminicola* Wollenweber is the same species as *Nectria graminicola* Berk. & Br. There is little evidence to support this synonymy and the perithecial state of the snow mould is better referred to as *Calonectria nivalis* Schaffn. or *Griphosphaeria nivalis* (Schaffn.) Müller & von Arx.

*Nectria graminicola* must be considered as a nomen dubium or as a probable synonym of *Nectria arenula*.

*Nectria inundata* Rehm, in Weese, *Z. Gärungsphysiol.*, 1, pp. 146-147, 1912.

Weese (1912) identified a specimen on wood of *Prunus padus*, ex Herb. Kew, as this species. I have not found the material in Kew and there is no evidence that it was a British collection.

*Nectria inventa* Pethybridge, *Trans. Brit. mycol. Soc.*, vi, pp. 104-107, 1919.

*Verticillium cinnabarinum* (Corda) Reinke & Berth., *Zersetz. d. Kartoff.*, p. 63, 1879.

*Acrostalagmus cinnabarinus* Corda, *Icon. Fung.*, ii, p. 15, 1838.

*Nectria inventa* was shown by Pethybridge (1919) to be the perithecial state of the common mould *Verticillium cinnabarinum*. The ascospores have not since been grown, and the work therefore has not been verified. In fact, the three collections by Petch cited in this paper are apparently the only records of the perithecia since they were first described, and these are not in good condition. These collections have been compared with the little type material available for examination and are in close agreement with this and with Pethybridge's description.

For a full discussion of the conidial state, one is referred to the paper by Hughes (1951). Until adequate perithecial material is obtained there is no justification for pursuing Hughes's suggestion that *Sphaeria erythrella* provides an earlier epithet for *Nectria inventa*.

#### DESCRIPTION

The following description is slightly modified from Pethybridge.

The perithecia are seated on a small pseudoparenchymatous stroma developing in the outer tissues of the host and becoming erumpent. They are globose to ovate, yellow to blackish brown in colour and measure 220-500  $\mu$  in diameter and 250-300  $\mu$  high. The upper half is covered with rigid hairs. These are hyaline, septate, and 5-6  $\mu$  at the base, narrowing to a point at the apex. They resemble the bases of abortive conidiophores. In section, the lateral wall is 35-45  $\mu$  wide and composed of 7-9 layers of hexagonal to globose thin-walled cells 6-10  $\times$  4-6  $\mu$ , these cells are somewhat smaller and more compressed towards the inner layers.

The asci are cylindrical to clavate 60-100  $\times$  4-6  $\mu$ , with eight obliquely monostichous ascospores.

The ascospores are oblong to fusiform, hyaline, 1-septate, and measure 8-12  $\times$  3-3.5  $\mu$ .

## SPECIMENS EXAMINED

*Nectria inventa* folder Herb. I.M.I.

On *Solanum tuberosum*, Clifden, Galway, Ireland, G. H. Pethybridge, July 1915, Type coll. (51936).

*Nectria inventa* folder Herb. B.M. Nat. Hist.

On decaying stalks of *Brassica* sp. North Wootton, Norfolk, T. Petch, Nov. 35, Oct. 36, Dec. 42.

*Nectria lugdunensis* Webster, *Trans. Brit. mycol. Soc.*, xlii, 1959.

This is a new aquatic species of *Nectria* found in Britain and described by Dr. J. Webster but not yet published. It shows a closer relationship to some of the tropical nectrias than to the other British species.

*Nectria pandani* Tul., *Selecta Fung. Carp.*, iii, p. 71, 1865.

Recorded by W. G. Smith on *Pandanus odoratissimus* in the Palm House of Edinburgh Botanical Garden as a form of *Nectria ochroleuca*. This can hardly be considered as a British species.

*Nectria polyporina* Petch, *Trans. Brit. mycol. Soc.*, xxv, p. 169, 1941.

The type and only material of this species was found on *Fomes annosus*. The stromata break through the hard upper surface of the host and produce the perithecia in small groups. No associated conidia were observed, although further collections and life-history studies will presumably show it to belong to the *Episphaeria* group.

## DESCRIPTION

The perithecia occur in small groups on an erumpent psuedo-parenchymatous stroma 170–220  $\mu$  in diameter. They are yellowish red to red, ampulliform with a short neck, smooth-walled and measure 170–200  $\mu$  in diameter. In section the lateral wall is 30  $\mu$  wide and shows a gradation from the thick-walled globose to oblong cells 7–9  $\times$  3–6  $\mu$  in the outer region to the more elongate cells 9–12  $\times$  2–3  $\mu$  in the inner layers.

The asci are clavate with a rounded apex containing a ring, they measure 60–70  $\times$  7–8  $\mu$  and have eight ascospores which become distichous at maturity.

The ascospores are fusoid, hyaline, with a slightly larger upper cell, and measure 12–14  $\times$  3–4.5  $\mu$ .

*Nectria wegeliniana* (Rehm) Höhn., in Strasser, *Verh. zool.-bot. Ges., Wien*, iv, p. 604, 1905.

Rehm (1891) published his *Ascomyceten Exs.*, Fasc. xxx in *Hedwigia*, under No. 1045 he described *Nectria episphaeria* var. *wegeliniana* Rehm. The exsiccatum issued under No. 1045 was *N. episphaeria* (Tode) Fr. f. *wegeliniana* Rehm.

Höhnel (1905) raised this to specific rank misspelling the epithet as *Nectria wegeliana* Rehm, a misspelling since used by most mycologists.

Weese (1916) agreed with Höhnel, but stated that *Nectria episphaeria* var. *wegeliniana* in Allescher et Schnabel, *Fungi Bavar.* No. 240, is a distinct fungus allied to *N. appianata* (*N. purtonii*). However, this is not a Rehm determination

and has nothing to do with Rehm's error in describing it as var. *wegeliniana* and publishing it as forma *wegeliniana*.

Petch (1938) followed Höhnel's spelling when he transferred *N. wegeliiana* to *Dialonectria* as *D. wegeliiana* (Rehm) Petch. Examination of the collections cited by Petch shows them to be *N. magnusiana*. Rehm's material of *N. episphaeria* f. *wegeliniana* is on *Pseudovalsa berkeleyi*, and has clavate asci with very thick, rough-walled ascospores,  $16-19 \times 8-9 \mu$ . It is clearly distinct from *N. magnusiana*. I have found no British collections of *N. wegeliniana*.

*Nectria umbrina* Berk., *Outl. Brit. Fung.*, p. 394, 1860.

*Sphaeria umbrina* Berk. in Smith's *Eng. Fl.*, v, 2, p. 264, 1836.

Described on 'decaying bean-stalks, Dec., Apethorpe, Norths., M. J. Berkeley'.

The 'type' and one other collection by Rev. Keith are the only ones found in the British Herbaria. Both are fragmentary and no *Nectria* is present. Höhnel and Weese (1910) stated that this was not a *Nectria*.

#### BRITISH RECORDS AS NECTRIA NOW EXCLUDED

<i>Nectria affinis</i> (Grev.) Cooke . . . . .	<i>Paranectria affinis</i> (Grev.) Sacc.
<i>Nectria albertini</i> Berk. & Br. . . . .	<i>Hypomyces rosellus</i> (Alb. & Schw. ex Fr.) Tul.
✓ <i>Nectria erubescens</i> (Rob. in Desm.) Bucknall	<i>Calonectria erubescens</i> (Rob. in Desm.) Sacc.
<i>Nectria furfurella</i> Berk. & Br. . . . .	<i>Pseudonectria furfurella</i> (Berk. & Br.) Petch
<i>Nectria helminthicola</i> Berk. & Br. . . . .	<i>Letendraea helminthicola</i> (Berk. & Br.) Weese
<i>Nectria hirta</i> Bloxam . . . . .	<i>Trichonectria hirta</i> (Blox.) Petch
✓ <i>Nectria muscivora</i> Berk. & Br. . . . .	<i>Hyphonectria (Nectriopsis) muscivora</i> (Tul.) Petch
<i>Nectria ochraceopallida</i> (Berk. & Br.) Sacc.	<i>Calonectria ochraceopallida</i> (Berk. & Br.) Sacc.
<i>Nectria ornata</i> Massee & Salm. . . . .	<i>Neohenningsia suffulta</i> (Berk. & Curt.) Petch
<i>Nectria peltigerae</i> Phil. & Plowr. . . . .	<i>Nectriella robergei</i> (Mont. & Desm.) Weese
<i>Nectria platasca</i> Berk. . . . .	<i>Calonectria platasca</i> (Berk.) Sacc.
<i>Nectria plowrightiana</i> Cooke & Plowr. . . . .	<i>Calonectria ochraceopallida</i> (Berk. & Br.) Sacc.
<i>Nectria pulicaris</i> (Fr.) Cooke . . . . .	<i>Gibberella pulicaris</i> (Fr.) Sacc.
<i>Nectria rosella</i> (Alb. & Schw. ex Fr.) . . . . .	<i>Hypomyces rosellus</i> (Alb. & Schw. ex Fr.) Tul.
✓ <i>Nectria rousseiliana</i> Mont. . . . .	<i>Pseudonectria rousseiliana</i> (Mont.) Wr.
✓ <i>Nectria suffulta</i> Berk. & Curt. . . . .	<i>Neohenningsia suffulta</i> (B. & C.) Höhn.

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## HOST INDEX

## ANGIOSPERMAE

*Host limited*

## Berberis

*Thyronectria lamyi*

## Brassica

*Nectria brassicae**Nectria keithii*

## Buxus

*Nectria desmazierii*

## Fagus

*Nectria ditissima* (canker forming)

## Hedera

*Nectria hederæ**Nectria sinopica*

## Ilex

*Nectria aquifolii**Nectria punicea* var. *ilicis*

## Rhamnus

*Nectria punicea*

## Ribes

*Thyronectria berolinensis*

## Rubus

*Nectria mammoidea* var. *rubi*

## Solanum

*Nectria inventa**Nectria solani**Nectriopsis solani*

## Ulmus

*Nectria aurantiaca**Not host limited*

## Herbaceous plants and shrubs

*Nectria arenula**Nectria ellisii**Nectria mammoidea*

## On Trees

*Nectria arenula**Nectria cinnabarina**Nectria coccinea**Nectria coryli**Nectria galligena* (canker forming)*Nectria mammoidea**Nectria mammoidea* var. *rugulosa**Nectria pallidula**Nectria peziza**Nectria ralfsii**Nectria veuillotiana**Nectria viridescens*

## GYMNOSPERMAE

## Pinaceae

*Nectria fockeliana**Nectria pinea**Nectria rishbethii**Nectria viridescens**Scoleconectria cucurbitula**Thyronectria balsamea*

## Taxaceae

*Nectria coccinea*

## FUNGI

## Ascomycetes

Diaporthaceae—*Nectria flavo-viridis*Diatrypaeae—*Nectria episphaeria*—*Nectria magnusiana*Meliolaceae—*Nectria aureola*Valsaceae—*Nectria purtonii*Xylariaceae—*Nectria episphaeria*

## Basidiomycetes

Polyporaceae—*Nectria peziza**Nectria polyporina*

## LICHENS

*Nectria lecanodes*

## MISCELLANEOUS

Manufactured cellulose, &amp;c.

*Nectria funicola**Nectria peziza*



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 — *sanguinea*, 74, 76, 84, 87, 89.  
 — *sinopica*, 6, 7, 8, 12-14, 112.  
 — *solani*, 34, 35, 39-41.  
 — *subquaternata*, 35, 38, 39.  
 — *suffulta*, 110.  
 — *tiliae*, 29.  
 — *umbrina*, 110.  
 — *verruculosa*, 32, 34.  
 — *veuillotiana*, 41, 42, 62, 68-70, 98.  
 — *viridescens*, 72, 73, 87, 89-92, 107.  
 — *viticola*, 73, 76.  
 — *wegeliniana*, 80, 81, 109-10.  
*Nectriella aureola*, 105.  
 — *bloxami*, 99.  
 — *charticola*, 104.  
 — *funicola*, 104.  
 — *graminicola*, 107.  
 — *robergei*, 110.  
*Nectriopsis aureonitens*, 35.  
*Neohenningsia suffulta*, 110.  
*Neuronectria peziza*, 96.

- Ophionectria cerea*, 15.  
— *cylindrospora*, 15, 18, 57.  
— *cylindrospora* var. *tetraspora*, 20.  
— *mellina*, 14–15.  
— *paludosa*, 14, 15.  
— *scolecospora*, 15, 16, 18.  
— *trichospora*, 14, 15.
- Paranectria affinis*, 110.  
*Pleonectria berolinensis*, 23, 25.  
— *calonectrioides*, 20.  
— *lamyi*, 19, 22, 23.  
— *pinicola*, 20.  
— *ribes*, 25.  
*Pseudonectria furfurella*, 110.  
— *rousseliana*, 110.
- Scolecnectria balsamea*, 19.  
— *cucurbitula*, 6, 7, 10, 15–19, 22, 43, 57, 70.  
— *scolecospora*, 16, 18, 19.
- Sphaeria abietis*, 82.  
— *aquifolii*, 4, 7, 9–10.  
— *arenula*, 99–100.  
— *cinnabarina*, 4, 27.  
— *coccinea*, 11, 42, 43, 45, 47, 48.  
— *coccinea* var. *cicatricum*, 47.  
— *cucurbitula*, 15, 16, 18.  
— *decidua*, 45.  
— *decolorans*, 27, 29.  
— *episphaeria*, 4, 73, 76, 82, 87, 89.  
— *erythrella*, 108.  
— *flavida*, 103.  
— *funicola*, 104.  
— *lamyi*, 21, 23.  
— *lecanodes*, 103.  
— *mougeotii*, 12.  
— *offuscata*, 29.
- Sphaeria peziza*, 4, 95, 97, 98.  
— *pinastri*, 82.  
— *punicea*, 52.  
— *purtonii*, 82, 84.  
— *ribis*, 23, 24, 25, 27.  
— *sanguinea*, 74, 76.  
— *sanguinea* var. *cicatricum*, 77, 79.  
— *sinopica*, 12, 14.  
— *umbrina*, 110.
- Sphaeronaemella mougeotii*, 12.  
*Sphaeronema hederæ*, 12, 14.  
*Sphaeropsis henricusii*, 32.  
*Sphaerostilbe aurantiaca*, 26, 29, 32.  
— *flammeola*, 84.  
— *flavo-viridis*, 86, 89.  
— *sanguinea*, 68, 70.
- Spicaria solani*, 39.  
*Stilbella aurantiaca*, 30.  
*Stilbum aurantiacum*, 29.  
*Stylonectria appianata*, 82.
- Thyronectria balsamea*, 6, 7, 15, 19–21.  
— *berolinensis*, 6, 7, 19, 23–26.  
— *lamyi*, 6, 7, 15, 19, 21–23.  
— *patavina*, 19.
- Tremella aurantiaca*, 80.  
— *elegans*, 80.  
— *purpurea*, 27, 80.
- Trichonectria hirta*, 110.  
*Tubercularia vulgaris*, 3, 24, 27, 80.  
*Tubeufia helicomyces*, 15.
- Verticillium cinnabarinum*, 108.
- Zythia mougeotii*, 12.  
— *pinastri*, 16.  
*Zythiostroma mougeotii*, 12.  
— *pinastri*, 16, 19.

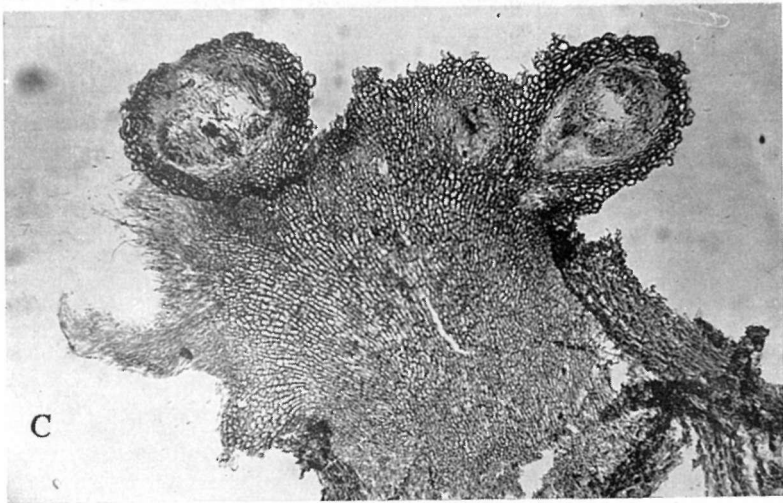
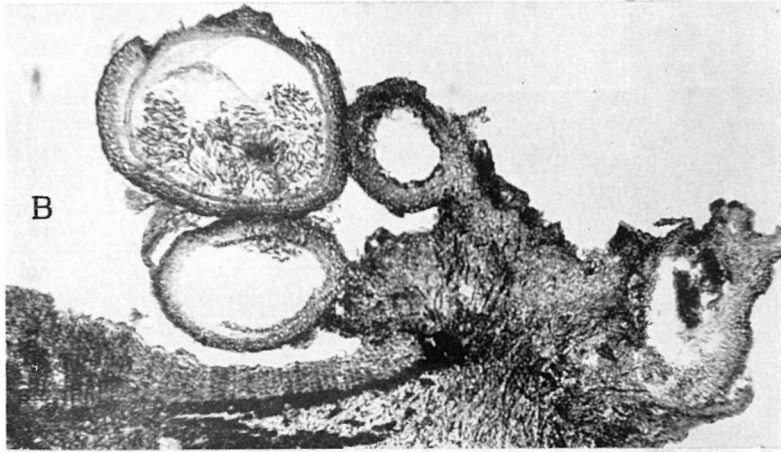
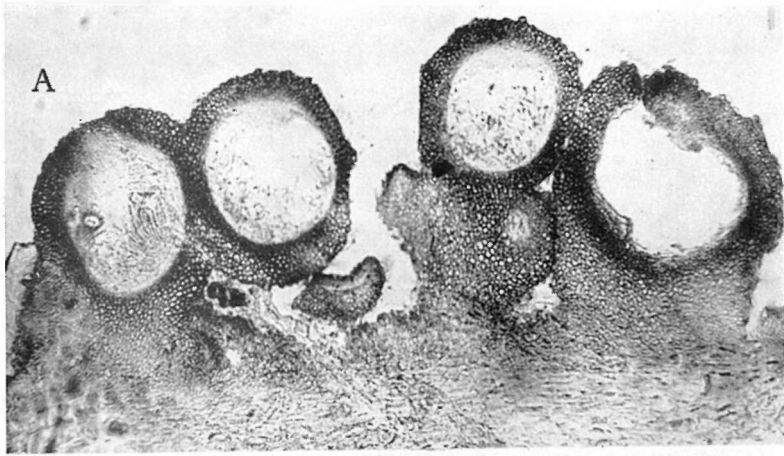


PLATE 1

A, *Nectria aquifolii*; B, *Nectria pallidula*; C, *Nectria cinnabarina*;  $\times 150$

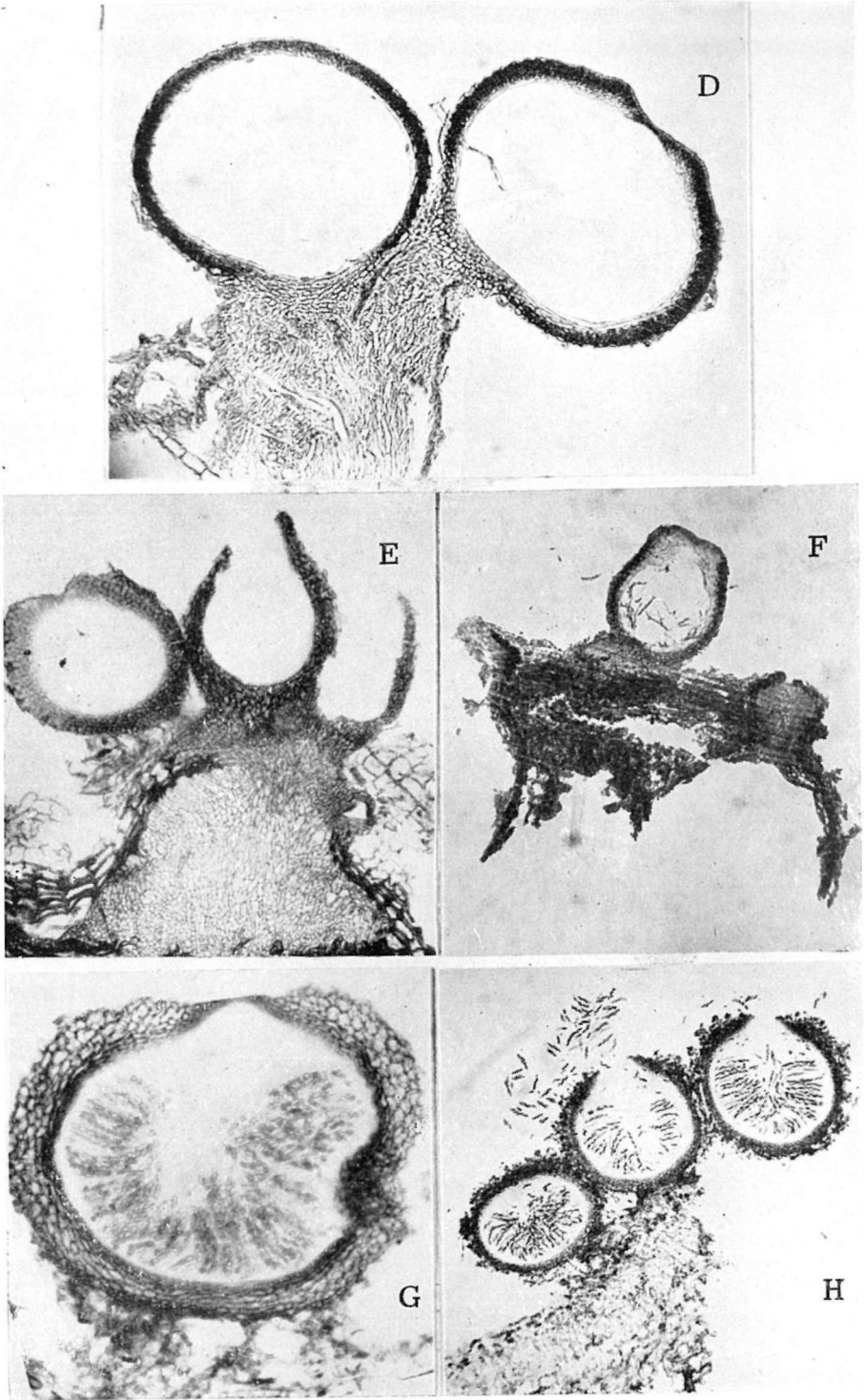


PLATE 2

D, *Nectria mammoidea*; E, *Nectria coccinea*; F, *Nectria episphaeria*; G, *Nectria peziza*;  
 H, *Nectria lecanodes*;  $\times 150$