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TAXONOMY OF *NEMATOGONUM, GONATOBOTRYS, GONATOBOTRYUM* AND *GONATORRHODIELLA*

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Type studies using light and scanning electron microscopy were made of *Nematogonum* and nine related hyphomycete genera containing over 40 described species, several of which are known contact mycoparasites. Three genera are accepted, distinguished by conidial development and secession (presence or absence of conidial chains and separating cells), with, in all, seven species (*Nematogonum ferrugineum*, *N. mycophilum* (Sacc.) comb.nov., *Gonatobotrys simplex*, *G. complex* sp.nov., *Gonatobotryum fuscum*, *G. parasiticum* (Thaxt.) comb.nov. and *G. apiculatum*). A key, descriptions and illustrations of these are provided, with a list of excluded taxa.

Fungi living as saprophytes or parasites on other fungi may be grouped according to their various means of deriving nutrition (Barnett & Binder, 1973). One group, the contact mycoparasites, characteristically lack haustoria, having instead specialized short hyphae which surround host cells and extract nutrients, at least in some species, by way of plasmodesmata (Hoch, 1977, 1978). Six species of contact mycoparasites are known, all hyphomycetes (Barnett, 1958; Butler & McCain, 1968; Gain & Barnett, 1970; Marvanová, 1977; Shigo, 1960; Whaley & Barnett, 1963), but many more may be undiscovered (Barnett & Binder, 1973). Of the six known species, *Nematogonum ferrugineum* (Pers.) Hughes, *Gonatobotrys simplex* Cda and *Gonatobotryum fuscum* (Sacc.) Sacc. form a distinct group with swollen terminal and intercalary conidiogenous cells, each of which produces conidia in large numbers, often in chains. There is growing interest in the possibility of using mycoparasites as biological control agents of fungal pests. During an investigation into parasitism of *Nectria coccinea* (Pers. ex Fr.) Fr., an ascomycete considered by some to be implicated in beech bark disease (Ayers, 1941; Ehrlich, 1942), by *N. ferrugineum*, isolates proved difficult to identify and the literature was found to be confused. The present study was therefore undertaken to provide a modern taxonomic treatment of this group of genera.

Examination of the literature revealed within the scope of this work over 40 specific epithets distributed between 9 genera. Where possible, type specimens of these taxa were examined and typification problems sorted out. Type material of some taxa was unavailable or could not be traced. In such cases it was often possible to make some decision based on the original description, accompanying illustrations or comments made by earlier workers. When available, other specimens apart from types were also examined. For examination under the scanning electron microscope, specimens were critical-point-dried and gold coated in a cool-stage sputter coater, or merely gold coated direct from dried herbarium material. Electron microscopy was used to evaluate the significance of characteristics visible under the light microscope. No taxonomic distinctions requiring electron microscopy for detection are made in this paper. Of the 40 specific epithets, all but six could be excluded as later synonyms, nomina dubia or as species belonging correctly in genera outside the scope of this work. Similarly, of the nine genera, five could be excluded immediately, and after careful consideration a further one was also excluded. These taxa are listed at the end of the paper or as synonyms of accepted taxa. In addition, one new species is described.

The evolution of generic concepts within this group centres on the three accepted genera (*Nematogonum* Desm., *Gonatobotrys* Cda and *Gonatobotryum* Sacc.) and the one which was eventually discarded (*Gonatorrhodiella* Thaxt.). Under the system of classification proposed by

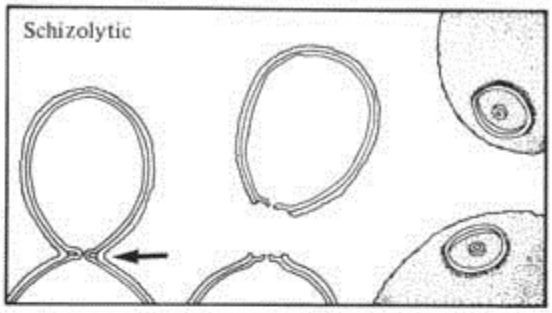


Fig. 1

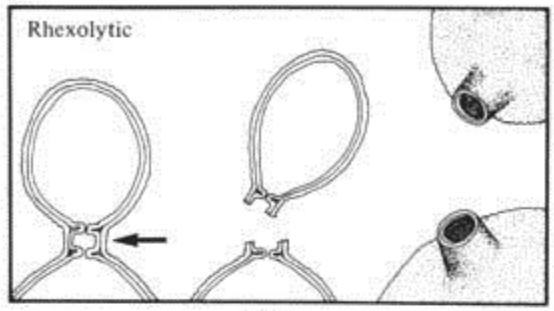


Fig. 2

Fig. 1. Schizolytic secession. The inner and outer cell walls split along the plane of weakness provided by the septum (arrowed), leaving inconspicuous scars on the conidium and conidiogenous cell.

Fig. 2. Rhexolytic secession. A separating cell delimited by two septa splits (arrow) and the two halves form conspicuous denticles on the conidium and conidiogenous cell.

Saccardo (1886), the four genera were separated using the following characteristics: *Nematogonum* (hyaline, conidia in branched chains), *Gonatorrhodiella* (hyaline, conidia in simple chains), *Gonatobotryum* (pigmented, conidia in branched or simple chains) and *Gonatobotrys* (hyaline, conidia not in chains). In proposing a new system of classification based on conidium ontogeny, Hughes (1953) reduced *Gonatorrhodiella* to synonymy with *Nematogonum*, which he viewed as being hyaline with simple or branched chains of conidia. He kept *Gonatobotryum* and *Gonatobotrys* apart, however, because the pigmentation in the one and the lack of chains in the other provided a convenient means of separation. Subsequently Kendrick, Cole & Bhatt (1968) expressed the view that pigmentation was not a characteristic of generic significance in this group. They suggested that *Gonatobotryum* should be reduced to synonymy with *Nematogonum*, leaving two genera (*Nematogonum* and *Gonatobotrys*) distinguished by the presence or absence of conidial chains. They did not, however, implement this proposal.

Since then there has been no taxonomic revision of these fungi, and their present disposition between genera therefore reflects the emphasis placed by Hughes (1953) on conidium ontogeny in hyphomycete taxonomy. Other developmental characteristics besides conidium ontogeny are now, however, also considered significant. Among these conidial secession has in recent years been the subject of several pertinent studies. Conidial secession is generally thought to come about in two ways (Cole & Samson, 1979), shown diagrammatically in Figs 1 and 2. In schizolysis the conidia secede by the splitting of the outer and inner cell walls along a plane of weakness provided by the septum. In rhexolysis special separating cells are produced which are destroyed when the conidia are released. Cole (1973), in a detailed study of *Gonatobotryum apiculatum* (Peck) Hughes one of the seven species accepted here, demonstrated, using light, scanning and transmission electron microscopy, that the conidia secede by rhexolysis, and speculated that this mode of secession is of significance within this group. Cole & Samson (1979) considered that conidia of *Gonatobotrys simplex* and *Nematogonum ferrugineum* probably secede by rhexolysis, but made no detailed study of either species. In view of these findings and speculations, the developmental characteristics of the seven accepted species are evaluated below.

CONIDIOPHORE DEVELOPMENT

All seven species produce conidiophores morphologically distinct from vegetative hyphae. These conidiophores are mostly erect and may be terminal or lateral. Conidiogenous cells are initially terminal but usually become intercalary by further growth of the conidiophore. This further growth may begin in two ways. In one the outer wall of the conidiogenous cell is continuous with the outer wall of the new growth (Fig. 3) and is described here as continuous. In the other an inner wall of the conidiogenous cell breaks out to form the outer wall of the new growth (Fig. 4) and is described here as percurrent. Continuous growth has been observed in all, and percurrent growth in six of the seven species. Percurrent growth was first observed in this group in *G. fuscum* by Bainier (1907). It probably also occurs in the seventh species, *G. simplex*, the hyaline conidiogenous

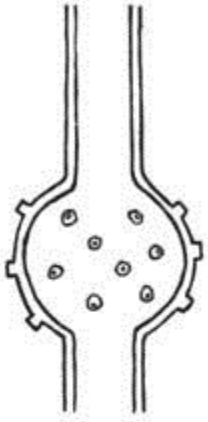


Fig. 3

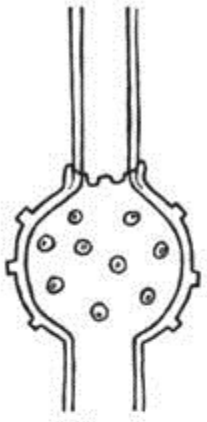


Fig. 4

Fig. 3. Continuous conidiophore growth. The outer wall of the conidiogenous cell is continuous with the outer wall of the new growth.

Fig. 4. Percurrent conidiophore growth. An inner wall of the conidiogenous cell breaks out to form the outer wall of the new growth. The edge of the broken outer wall is usually ragged.

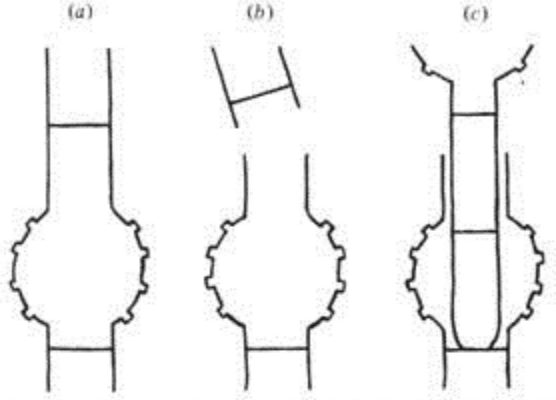


Fig. 5. Regeneration. An intact conidiophore (a) is decapitated (b) and regrowth occurs from the highest intact cell (c).

cells of which have made detection of this feature difficult. In all seven species the production of a succession of new terminal conidiogenous cells by continuous or percurrent growth appears to be the result of proliferation, i.e. it is a feature of normal growth under continuously favourable conditions. Regeneration by further growth following damage or some other event unfavourable to the fungus can also occur. Such regeneration seems to be invariably percurrent. Examples have been seen of decapitated conidiophores where regrowth occurs from the highest intact cell (Fig. 5).

CONIDIUM ONTOGENY

In all species the conidia are produced holoblastically from more or less swollen conidiogenous cells each bearing a variable but large number of conidiogenous loci. In *G. simplex* and *G. complex*, a single conidium arises from each locus; in *G. fuscum* two conidia in a simple chain; in *Gonatorrhodiella parasitica* Thaxt. three conidia in a simple chain, and in the remaining three species usually more than three conidia in branched chains characteristic for each species. Kendrick *et al.* (1968) using time-lapse photography have shown that in *G. apiculatum* the conidia proximal to the conidiogenous cells develop simultaneously, then give rise asynchronously to subsequent conidia. None of the other six species has been studied in this way but, judging from the literature (Ali, 1975) and herbarium specimens, it seems likely that conidia of *G. simplex* and *G. complex* and proximal conidia of *G. fuscum* and *G. parasitica* also arise simultaneously. The situation is less clear for proximal conidia of *N. ferrugineum* and *N. mycophilum* (Sacc.) Rogerson & W. Gams, but in some specimens of the former, conidia from loci lower down the conidiogenous cell appear to develop later than those from higher up. Bainier (1880), however, in an early but careful study of *N. ferrugineum* reported that the proximal conidia develop synchronously. Nothing is known of the timing of development of subsequent conidia in these species.

CONIDIAL SECESSION

In *N. ferrugineum* conidia are delimited from the conidiogenous cell and each other by single septa (Fig. 15). We observed no separating cells in this species. After secession the scars are usually inconspicuous, sometimes invisible, although occasional conidia may bear a small hilum. Scanning electron micrographs of seceding conidia (Fig. 17) and the resulting scars (Figs 16, 18–19) are consistent with the expected appearance of scars caused by schizolysis (Fig. 1). We have therefore been unable to verify Cole & Samson's (1979) speculation that *N. ferrugineum* is rhexolytic. Light microscopy of *N. mycophilum* indicates that its conidia probably secede similarly to those of *N. ferrugineum*.

Conspicuous separating cells are present in *G. simplex*. The separating cells appear to be delimited by two septa, although this has not been

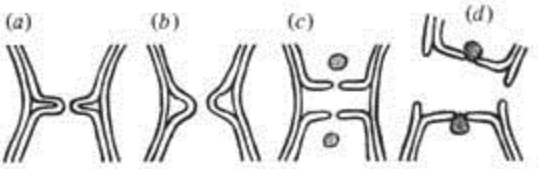


Fig. 6. A model of how separating cells might occur in an apparently schizolytic secession. A septum is formed (*a*), stretching occurs (*b*), the inner wall which forms the septum breaks before the septum is plugged and while the outer wall remains intact. A 'separating cell' lined by only an outer wall is thus formed (*c*). The septum is plugged and the conidium finally secedes, leaving small denticles on both conidium and conidiogenous cell (*d*).

verified using the transmission electron microscope. After secession the remains of each broken separating cell can be seen on the conidium and conidiogenous cell as denticles (Figs 23–24) which are more or less conspicuous, depending on the point at which splitting occurred. These denticles can become less conspicuous with age and are often harder to detect on intercalary conidiogenous cells lower down the conidiophore. Scanning electron micrographs of denticles (Figs 20–22) are consistent with the expected appearance of denticles caused by rhexolysis (Fig. 2) and we agree with Cole & Samson's (1979) suggestion that conidial secession in this species is rhexolytic. *Gonatobotrys complex* appears under the light and scanning electron microscopes to be similar. *Gonatobotryum apiculatum* is also rhexolytic (Cole, 1973) and has conspicuous separating cells (Figs 35–42).

In *G. fuscum* and *G. parasitica* inconspicuous separating cells are present between adjacent conidia and the conidiogenous cells. Although developing conidia are delimited in *G. fuscum* by a single dark line (Fig. 32), the separating cell between mature conidia can be seen under the light microscope to be delimited by two dark lines (Fig. 32, arrow) and following secession the denticles, although small, are easily seen because of this darkening. The appearance of these denticles under the scanning electron microscope is, however, problematical (Fig. 29) and cannot unequivocally be interpreted as resulting from either schizolysis or rhexolysis. Darkening is absent from *G. parasitica*, but the conidia appear to secede similarly.

DISCUSSION

Not all developmental characteristics are of equal value in assigning these species to appropriate genera. Conidiophore development, proliferation and regeneration are similar in all seven and, in our opinion, provide no characteristics suitable for identifying species, let alone genera. It is interesting to compare this with the situation in *Endophragmiella* Duvernoy & Maire and related genera in which Hughes (1979) has shown conidiophore proliferation and regeneration to be significant.

Since all seven species produce holoblastic conidia, this aspect of conidial ontogeny is of no value at specific or generic level within the group, although it is important in distinguishing this group from genera such as *Aspergillus* Micheli ex Link which are superficially similar in shape. The presence or absence of chains, and the type of chain produced are characteristic for each species, and have also been used in the past at generic level. Such use seems arbitrary, however, as examples are known of every stage between single conidia and long and complex chains, and it might be argued, for example, that species producing a fixed number of conidia from a given conidiogenous locus are more closely related to each other than to species producing an indefinite number. In his recent treatment of *Sporothrix* Hektoen & Perkins ex Nicot & Mariat, de Hoog (1974) considered the presence or absence of chains was not in itself necessarily a characteristic of generic significance.

The conidial secession of five of the seven species can be explained adequately by the two types of secession postulated by Cole & Samson (1979). That of the remaining two species (*G. fuscum* and *G. parasitica*) is less clear. The separating cells are very small, and seem to originate from one septum, i.e. the dark line delimiting developing conidia as seen in *G. fuscum*. This suggests that, although intermediate stages have not hitherto been reported, the distinction between schizolysis and rhexolysis is not clear cut. A model of how separating cells might occur in an apparently schizolytic secession is shown in Fig. 6. Secession in *Ramularia rhombica* Matsushima and *R. fusisaprophytica* Matsushima as illustrated by Matsushima (1975), in *Cladosporium sphaerospermum* Penz. as illustrated by Cole & Samson (1979), and in *G. fuscum* and *G. parasitica* could be explained by this or a similar model. A transmission electron microscope study is in progress to examine wall relations in the separating cells of *G. fuscum*.

The swollen conidiogenous cells of the five species with separating cells appear strikingly similar to those of *Oedocephalum* Pr. and suggest a relationship. This similarity was first observed by Harz (1871), and was later discussed also by Matruchot (1892) and Vuillemin (1911). In the

past *Oedocephalum* was distinguished because it produces solitary terminal conidiogenous cells, whereas in the five species with separating cells proliferation occurs, making the conidiogenous cells intercalary. Although Stalpers (1974) reported that some species of *Oedocephalum* can proliferate occasionally, this remains a convenient means of keeping it apart. Catenate conidia are unknown in *Oedocephalum*, but are considered here not necessarily of generic significance. Developmental studies have shown that in *Oedocephalum* conidia develop synchronously (Cooke, 1974) a characteristic of proximal conidia of the five species here. The conidia of *Oedocephalum* are delimited by a single septum (Cooke, 1974), an important feature in distinguishing it from *G. simplex*, *G. complex* and *G. apiculatum*, and suggesting that it is most closely related to *G. fuscum* and *G. parasitica*. Teleomorphs of *Oedocephalum*, where known, occur in the Pezizales. Teleomorphs of *G. fuscum* and *G. parasitica* are not known but, if discovered, it would not be surprising to find they were operculate discomycetes.

The comparison of the species given above shows that they fall into two main groups, with or without separating cells. These two groups can easily be distinguished under the light microscope by the inconspicuous scars or conspicuous denticles on the conidiogenous cells. The two species without separating cells (*N. ferrugineum* and *N. mycophilum*) are clearly closely related. Of the five species with separating cells, two (*G. fuscum* and *G. parasitica*) are closely related and have a different type of separating cell from the other three, of which two (*G. simplex* and *G. complex*) are closely related, and the third (*G. apiculatum*) is unrelated to any of the other species. Four genera would be ideal to reflect these relationships: one containing *N. ferrugineum* and *N. mycophilum*, another containing *G. fuscum* and *G. parasitica*, a third with *G. simplex* and *G. complex* and the fourth containing *G. apiculatum*. Had we found more acceptable species than the seven with which we were left, this would have been tempting. In view of Kendrick's (1980) remarks, however, four genera for seven species is probably excessive, particularly as such a course would necessitate the erection of a new genus for *G. apiculatum*. Amalgamating all seven species into a single genus is equally undesirable. Such a genus would be too diverse morphologically and probably also phylogenetically. We have chosen a central course, recognizing three genera: *Nematogonum* (separating cells absent), *Gonatobotrys* (separating cells present, conidia not in chains) and *Gonatobotryum* (separating cells present, conidia in chains). Under such an arrangement, although *Gonatobotryum* remains diverse, the number of nomenclatural changes is minimized, so that most of the previous research on these fungi will be found under the names accepted here.

Key to species of Nematogonum, Gonatobotrys and Gonatobotryum

1 Conidia not in chains 2
1 Conidia in chains 3

2 Conidia aseptate . . . . . *Gonatobotrys simplex*
2 Conidia septate . . . . . *Gonatobotrys complex*

3 Separating cells absent, scars on both conidiogenous cells and conidia inconspicuous 4
3 Separating cells present, leaving conspicuous denticles on conidiogenous cells and more or less conspicuous denticles on conidia. 5

4 Conidia ellipsoid, joined by a narrow isthmus 1 μm wide, colonies orange . . *Nematogonum ferrugineum*
4 Conidia doliiform, joined by a broad isthmus 3 μm wide, colonies white . *Nematogonum mycophilum*

5 Conidia in branched chains usually more than three long. . . . . *Gonatobotryum apiculatum*
5 Conidia in simple chains of two or three 6

6 Conidia and conidiophores lightly pigmented or hyaline, conidia in chains of three, colonies white *Gonatobotryum parasiticum*
6 Conidia pale brown, conidiophores dark brown, conidia in chains of two, colonies dark brown *Gonatobotryum fuscum*

NEMATOGONUM Desm., *Annls Sci. nat.* II. **2**: 69 (1834).

Botryocladium Pr., *Linnaea* **24**: 134 (1851).

Mycelium hyaline, smooth, septate, branched, superficial. *Conidiophores* mononematous, macronematous, broad, erect, septate, hyaline to pale brown, smooth, thick-walled, usually unbranched, occasionally branching dichotomously with no main axis. *Conidiogenous cells* terminal, usually becoming intercalary by continuous or percurrent proliferation or by percurrent regeneration, integrated, hyaline to pale brown, smooth, thick-walled, producing conidia from up to about 20 loci. *Conidia* hyaline to pale brown, aseptate, rarely

1-septate, smooth, in branched chains up to 8 conidia long, distal conidia being smaller than the proximal ones. *Conidial ontogeny* holoblastic, polyblastic. *Conidial secession* without separating cells, schizolytic, leaving inconspicuous unblackened scars on the conidiogenous cells and conidia.

Type species: *Nematogonum ferrugineum* (Pers.) Hughes

Although the epithet '*ferrugineum*' is now used for the type species of this genus, because it is the earliest available, the typification of the genus depends on the type specimen of *Nematogonum aurantiacum* Desm., since this was the only species included by Desmazières in *Nematogonum* when he originally described the genus. *Nematogonum aurantiacum* is now regarded as a later, facultative synonym of *N. ferrugineum*. In the literature orthographic variants of *Nematogonum* appear, e.g. *Naematogonium* and *Nematogonium*.

It is interesting to note how *Nematogonum* and *Aspergillus* have been confused in the past. They are superficially similar, and this may explain the confusion in, for example, the case of *Aspergillus aureus* Berk., a synonym of *N. ferrugineum*. Although no specimen survives, *Aspergillus dessyi* Speg., the type species of *Thomiella* Dodge is, to judge from Spegazzini's illustration on the packet, another probable example of this confusion. The problem is complicated by the fact that both *Nematogonum* and *Aspergillus* are thought to be pleomorphic. Matsushima (1975) reported an *Aspergillus*-like anamorph for *Nematogonum highlei* (A.L.Sm.) Vuill. (a synonym of *N. ferrugineum*), although it is conceivable that the *Nematogonum* was parasitizing an *Aspergillus*-like fungus which he misinterpreted as an anamorph. Similarly *Aspergillus* mutants are known which produce holoblastic conidia in chains (Madelin, 1979) giving them a form very similar to *Nematogonum* species. The genus *Cladosarum* Yuill & Yuill has been used to accommodate these mutants. Further investigation into the relationship of *Nematogonum* and *Aspergillus* may be worthwhile.

NEMATOGONUM FERRUGINEUM (Pers.) Hughes, *Can. J. Bot.* **36**: 789 (1958). (Figs 7, 14–19)

Monilia ferruginea Pers., *Mycol. eur.* **1**: 30 (1822).

?Mucor ferrugineus Sow., *Engl. Fungi* **3**, tab. 378 (1803).

Nematogonum aurantiacum Desm., *Annls Sci. nat.* II. **2**: 69 (1834).

Aspergillus aureus Berk., *English Flora* **5**: 340 (1836).

Nematogonum aureum (Berk.) Berk., *Outl. Br. Fung.* p. 348 (1860).

Botryocladium delectatum Pr., *Linnaea* **24**: 134 (1851).

Nematogonum delectatum (Pr.) Sacc., *Syll. Fung.* **4**: 170 (1886).

Gonatorrhodiella highlei A.L.Sm., *Trans. Br. mycol. Soc.* **3**: 10 (1908).

Nematogonum highlei (A.L.Sm.) Vuill., *Bull. Soc. bot. Fr.* **58**: 169 (1911).

Colonies orange. *Conidiophores* 250–2000 × 8–18 μm. *Conidiogenous cells* usually swollen, clavate, individual swellings measuring 40–100 × 13–35 μm, individual cells sometimes comprising several such swellings as a result of proliferation. *Conidia* elliptical, 4–24 × 3–15 μm, becoming progressively smaller towards the tips of the chains which are usually repeatedly branched, narrowly attached by an isthmus about 1 μm wide.

Specimens examined: slide ex herb. Pers., isotype of *Monilia ferruginea* Pers., IMI 9354; on decaying wood and bark, Desm., 30c, No. 8 ex herb. Desm., holotype of *Nematogonum aurantiacum* Desm., PC; ex herb. Sowerby, holotype of *Aspergillus aureus* Berk., K; herb. Pr. 1155, lectotype of *Botryocladium delectatum* Pr., B; also IMI 6618, 8141, 12209, 18177, 18178, 18179, 18180, 35256, 61773, 194051, 217881, 217925, 246536, 246537, 246538.

Persoon (1822) referred to *Mucor ferrugineus* Sow., but doubted whether it was the same species as his *Monilia ferruginea*. No Sowerby collection labelled *Mucor ferrugineus* could be found in K, but in describing *Aspergillus aureus*, Berkeley speculated whether the type specimen had also been used by Sowerby to describe *Mucor ferrugineus*. The Sowerby collection which forms the holotype of *A. aureus* is a mononematous hyphomycete growing over *Nectria coccinea* on bark, and is clearly the same as *N. ferrugineum* (Pers.) Hughes. Sowerby's description and illustration of *Mucor ferrugineus*, however, suggest a synnematous fungus on mouldy hay. We therefore consider it unlikely that the type of *Aspergillus aureus* was used by Sowerby to describe *Mucor ferrugineus*, and since Sowerby's illustration is not an adequate type, we consider the epithet '*ferrugineum*' is best typified by the Persoon specimen, the isotype of which, cited above, is in poor condition. The specimen of *Botryocladium delectatum*, cited above, was selected by Hennebert as lectotype in a written note enclosed in the packet. We have not been able to trace original material of *Gonatorrhodiella highlei*. If Matsushima's (1975) treatment is followed, it is clearly a *Nematogonum* and, apart from the questionable *Aspergillus*-like anamorph, appears not to differ from *N. ferrugineum*. It is tentatively included here as a synonym of *N. ferrugineum*, but it is odd that the type

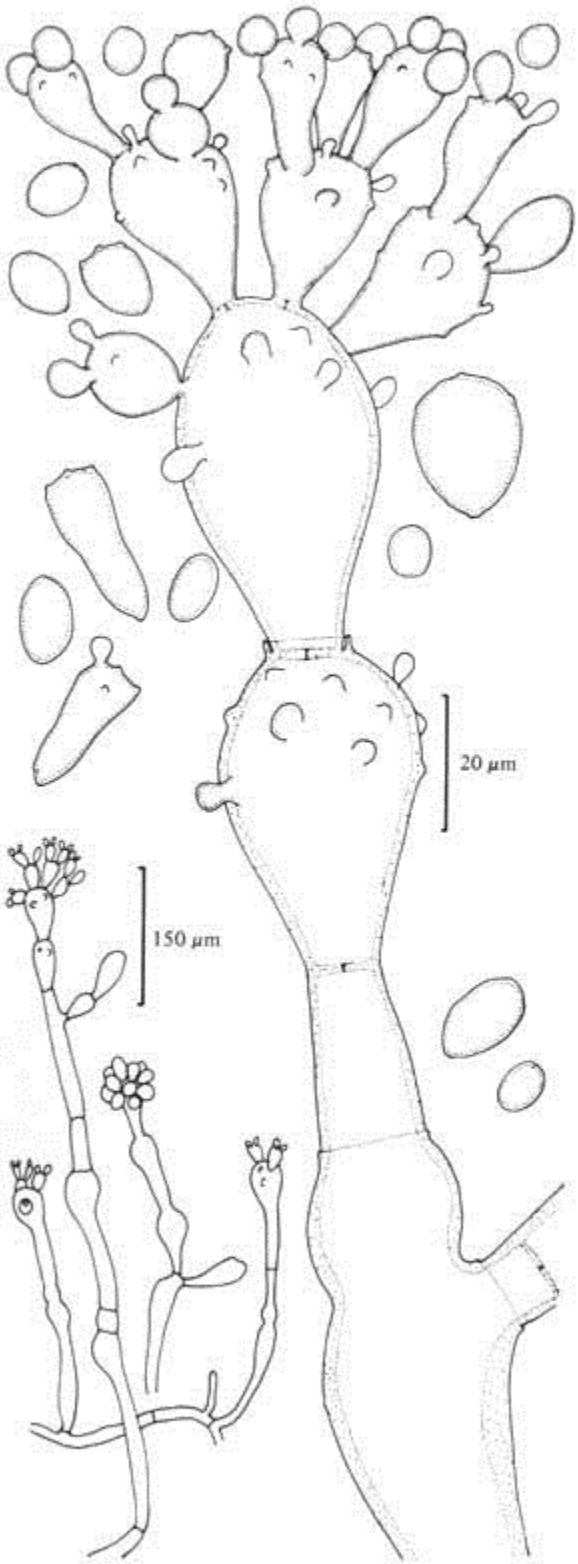


Fig. 7. *Nematogonum ferrugineum.*

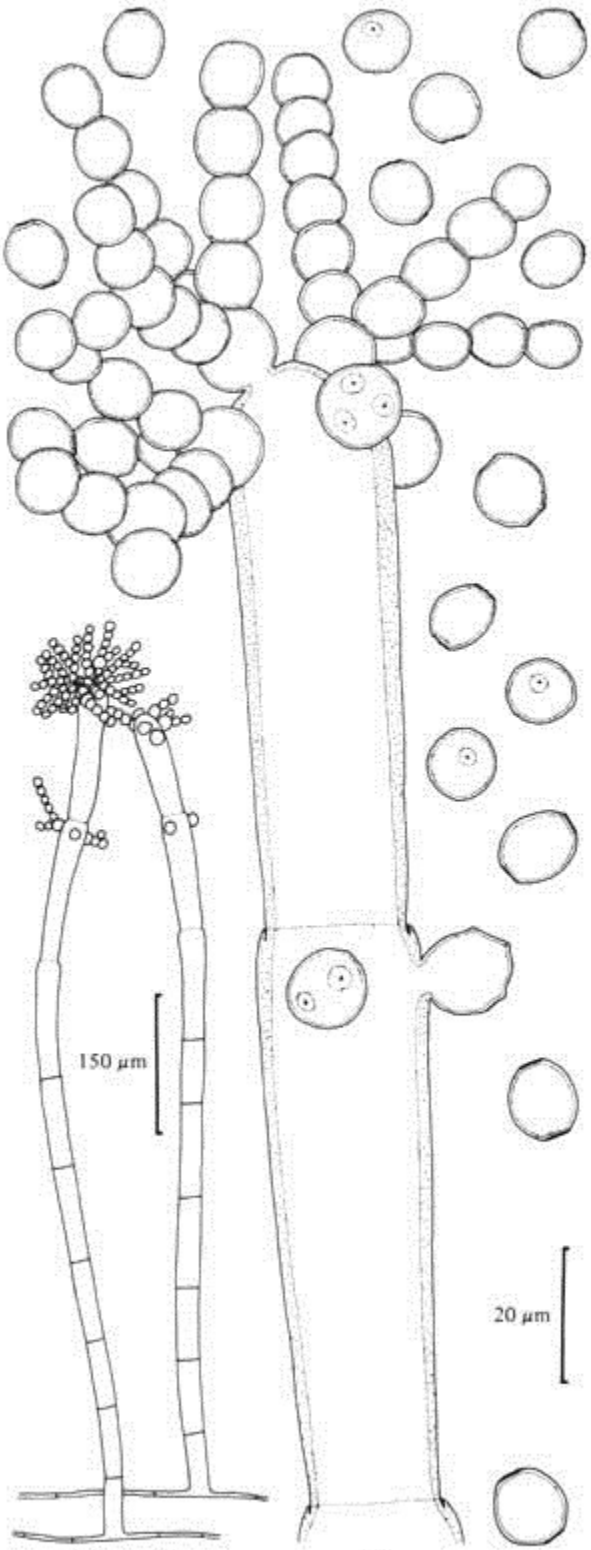


Fig. 8. *Nematogonum mycophilum.*

material of *G. highlei* was on corms of a monocotyledon whereas all specimens examined of *N. ferrugineum* were on woody plants, usually dicotyledons.

Nematogonum ferrugineum was originally described growing on dead wood and bark. It has subsequently been recorded under the various names given above growing on dead wood, bark and roots of various trees including *Castanea*, *Fagus*, *Juglans*, *Magnolia*, *Picea*, *Platanus*, *Populus*, *Quercus* and *Ulmus*, and on corms of *Allium*. It is known from Asia (Japan), Europe (Austria, Czechoslovakia, France, Germany, Great Britain, Italy) and North America (Canada: New Brunswick, Nova Scotia; the United States: Maine, New Jersey, Virginia). *Nematogonum ferrugineum* is now known to be a contact mycoparasite (Ayers, 1941; Blyth, 1949; Gain & Barnett, 1970; Ehrlich, 1942), and it is likely that in all the records given above it was growing not directly on the higher plant, but on another fungus. It is usually collected on *Nectria coccinea* and has been seen in association with the *Cylindrocarpon* anamorph of this species. Parasitism of other species of *Nectria* (Ayers, 1941; Blyth, 1949; Gams, 1975) and of species of *Chaetomella*, *Cladosporium*, *Graphium*, *Tritirachium* and *Verticillium* (Gain & Barnett, 1970) has also been demonstrated. Ayers (1941) speculated that *N. ferrugineum* was introduced from Europe to North America with *Nectria coccinea* which he believed was implicated in beech bark disease. Perrin (1977) reported the fungus (as *G. highlei*) on *N. coccinea* associated with beech bark disease from France. *Nectria coccinea*, *N. coccinea* var. *faginata* Lohman, Watson & Ayers, *N. ditissima* Tul., and *N. galligena* Bres. have all been associated with beech bark disease (Booth, 1977). Before biological control of beech bark disease by *Nematogonum* (Perrin, 1979) can seriously be considered, therefore, the species of *Nectria* on which *N. ferrugineum* can occur should be properly established.

Nematogonum mycophilum (Sacc.) Rogerson & W. Gams, comb.nov. (Fig. 8)

Monilia candida Peck, *Bull. N.Y. St. Mus.* **27**: 106 (1875). (Nom. illegit., art.64.)
Monilia mycophila Sacc., *Syll. Fung.* **4**: 35 (1886).
Nematogonum niveum W. Gams, *Revue Mycol.* **39**: 273 (1975).
Non *Monilia candida* Bonord., *Handb. Mykol.* p. 76 (1851).

Colonies white. *Conidiophores* 250–2750 × 18–30 μm. *Conidiogenous cells* usually not swollen, 100–220 × 20–35 μm, individuals comprising several proliferations are much longer. *Conidia* doliiform, those adjacent to the conidiogenous cells being larger, 12–17 × 9–14 μm, and tending to form branched chains; those in the chains being rather uniform and smaller, 6–11 × 5–10 μm, and branching less frequently, broadly attached by an isthmus about 3 μm wide.

Specimens examined: on decaying fungi, Forestburgh, Sullivan County, Catskill Mts., New York, U.S.A., Sept. 1873, holotype of *Monilia candida* Peck, NYS; Dried culture isolated from *Eleutheromyces subulatus* on decaying agaric, Plateau d'Albion, Revêt du Bion, France, Oct. 1974, W. Gams & H. A. van der Aa, holotype of *Nematogonum niveum*, CBS 0161.

Saccardo (1886) proposed the new name *Monilia mycophila* to replace *M. candida* Peck, which is a later homonym of *M. candida* Bonord. The holotype of Peck's species consists of fragmented cap and gills of an old agaric and sclerotia and sterile stipes of a species of *Collybia*. The *Nematogonum* is fairly abundant. This species is apparently uncommon, being known only from two collections. Although not established as a contact mycoparasite, it is significant that this species was isolated from *Eleutheromyces*, a coelomycete genus showing strong affinities with known anamorphs of *Nectria* and other members of the Hypocreaceae, suggesting that its host range is comparable to that of *N. ferrugineum*. Gams (1975) noted a more or less marked diurnal variation in conidium production in this species and *N. ferrugineum*.

GONATOBOTRYS Cda, *Pracht-fl.*: 9 (1839).
Desmotrichum Lév., *Annls Sci. nat.* II, **19**: 217 (1843).

Mycelium hyaline, septate, branched, superficial. *Conidiophores* mononematous, macronematous, broad, erect, septate, hyaline, smooth, thin-walled, unbranched or rarely branched. *Conidiogenous cells* terminal, usually becoming intercalary by continuous or percurrent proliferation or by percurrent regeneration, integrated, hyaline, smooth, thin-walled, globose, producing conidia from up to about 80 loci. *Conidia* hyaline, obovoid, aseptate or 1-septate, smooth or roughened, produced singly. *Conidial ontogeny* holoblastic, polyblastic, conidia developing synchronously. *Conidial secession* with separating cells, rhexolytic, leaving more or less conspicuous unblackened denticles on the conidia and conidiogenous cells.

Type species: *Gonatobotrys simplex* Cda

GONATOBOTRYS SIMPLEX Cda, *Pracht-fl.*: 9 (1839). (Figs 9, 20–24)
Desmotrichum simplex Lév., *Annls Sci. nat.* II, **19**: 217 (1843).

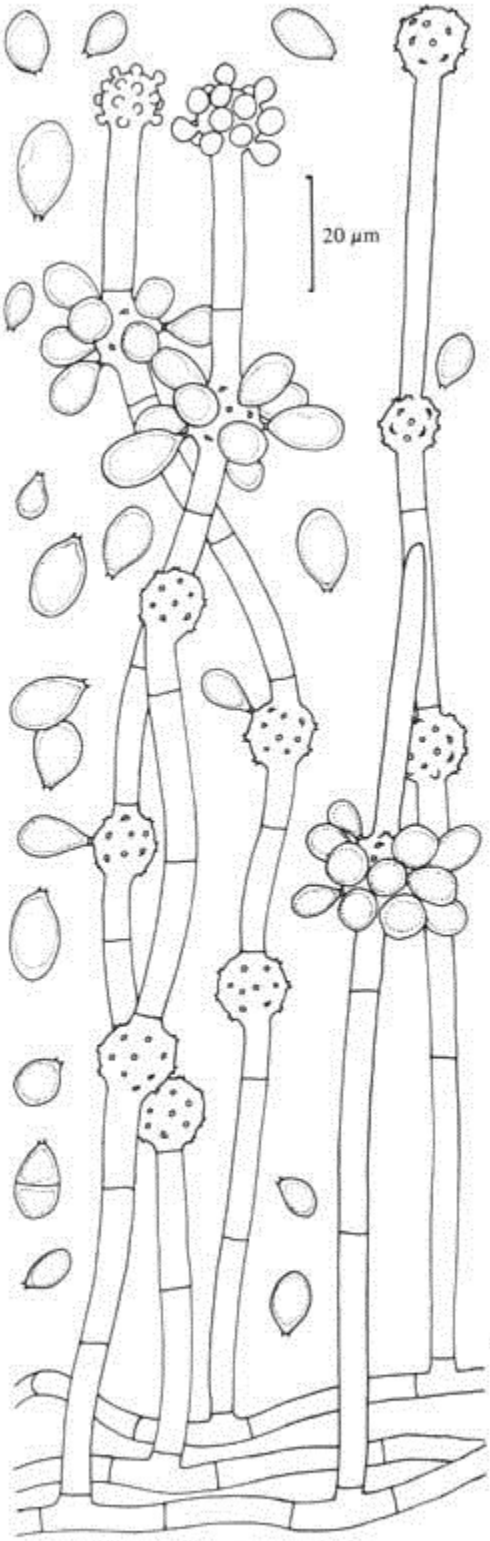


Fig. 9. *Gonatobotrys simplex.*

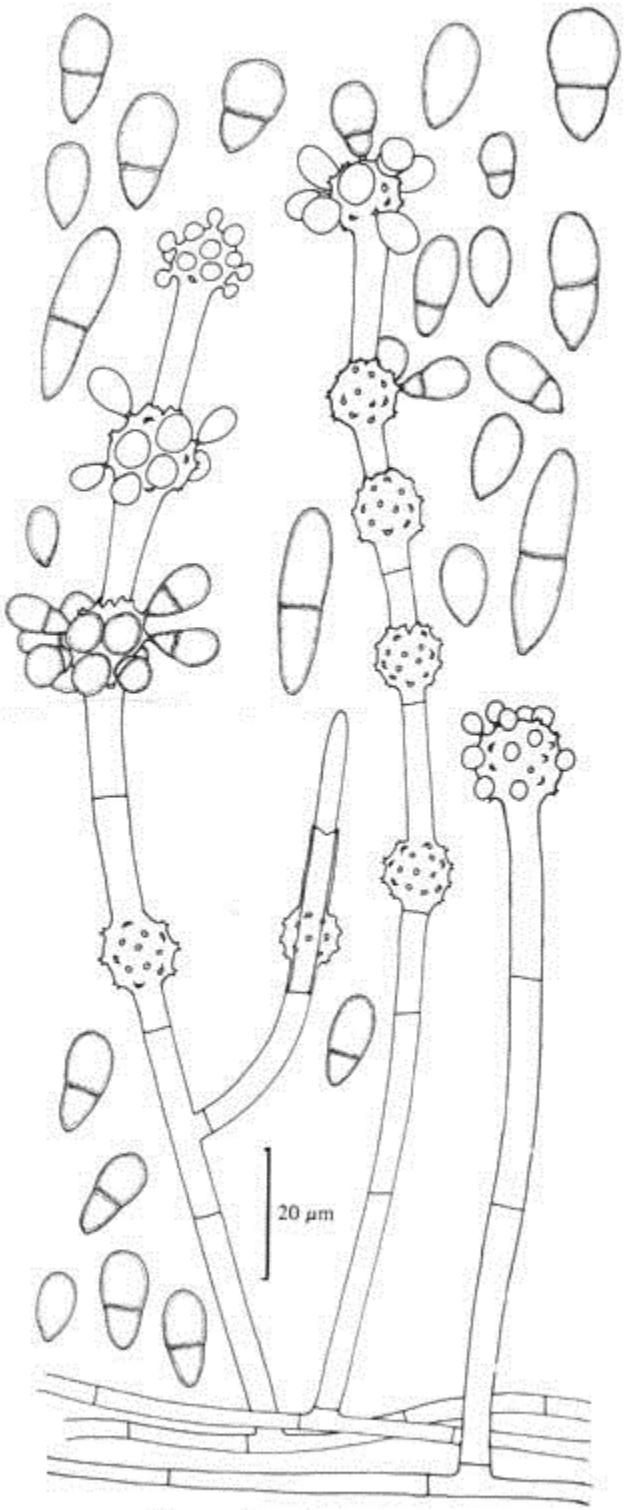


Fig. 10. *Gonatobotrys complex.*

Gonatobotrys simplex Cda var. *leveillei* Sacc., *Syll. Fung.* **4**: 170 (1886).

Colonies white. *Conidiophores* 250–1500 × 4–10 μm, probably sometimes even longer. *Conidiogenous cells* with a swollen part 10–18 × 7–14 μm. *Conidia* aseptate, 10–22 × 6–12 μm. Separating cells of this species tend to break near the conidiogenous cell, leaving large denticles on the conidium.

Specimens examined: PRM 155515, 155516 both ex herb. Cda; also IMI 384, 24953, 47700, 54373, 95759, 150178, 185424, 207197, 214533.

The specimens from Corda's herbarium, although being his original collections, are in a poor condition. Holubová examined them in 1972, and in written notes enclosed with the packets observed that only *Cladosporium* and *Alternaria* species were present. Neither specimen is therefore suited to be a type. The illustration accompanying the original description is, however, adequate, and we designate it as lectotype. Although we have been unable to trace any specimens of *Desmotrichum simplex* (≡*G. simplex* var. *leveillei*), the illustration accompanying the original description shows that it is clearly the same fungus as *G. simplex*. Matsushima (1975) treated a collection with conidia at the larger end of the range as *Gonatobotrys flava* Bonord., a species discussed in the list of excluded taxa at the end of this paper.

Corda originally described *G. simplex* as growing on *Helminthosporium* on dead bark. It is likely that the *Alternaria* found by Holubová on the original collections was Corda's '*Helminthosporium*', although Bainier (1907) and Vuillemin (1911) both believed Corda's fungus was *Clasterosporium*. Drechsler (1950) examined *G. simplex* as a possible nematophagous fungus on the grounds that it is morphologically similar to species of *Arthrobotrys* Cda. He failed to demonstrate parasitism of either nematodes or other fungi, and concluded that *G. simplex* was not related to *Arthrobotrys* species. Subsequently, however, Whaley & Barnett (1963) and later Hoch (1977) have shown convincingly that *G. simplex* is a contact mycoparasite of a variety of hyphomycetes including several species of *Alternaria*, *Cladosporium* and *Paecilomyces*, and Sutton (1973) has reported the fungus growing on *Dibotryon* and its *Cladosporium* anamorph. *Gonatobotrys simplex* has been collected in association with these fungi on leaves, stems, wood and bark of various angiosperms, including *Althaea*, *Citrus*, *Cucumis*, *Dalbergia*, *Fagus*, *Fragaria*, *Lycopersicon*, *Onobrychis*, *Pisum*, *Prunus*, *Pyrus*, *Rhododendron*, *Rosa*, *Rubus*, *Sorghum*, *Triticum* and *Ulmus* and has been isolated from desert soil. It is known from Africa (Egypt), Asia (Iraq, Japan), Australasia (New Zealand), Europe (Czechoslovakia, France, Germany, Great Britain) and North America (Canada: Manitoba; U.S.A.: Virginia).

Gonatobotrys complex Jane Walker* & Minter sp.nov. (Fig. 10)

A *G. simplici* differt quod conidia habet uniseptata.

Inter colonias *Alternariae* speciei in caulibus cuiusdam *Yuccae* speciei crescentes inventus, Red Feather Lakes, Colorado, U.S.A., 29 Aug. 1980, B. C. Sutton, IMI 252533b holotypus.

Colonies white. *Conidiophores* 250–1500 × 6–10 μm, probably sometimes even longer. *Conidiogenous cells* with a swollen part 9–15 × 9–15 μm. *Conidia* aseptate, soon becoming 1-septate, constricted at the septum, 10–40 × 9–12 μm. Separating cells of this species tend to break near the conidium, leaving large denticles on the conidiogenous cell.

Specimens examined: IMI 252533b holotype; among colonies of *Alternaria* sp. growing on stems of *Yucca glauca*, Buckthorn Canyon, Colorado, U.S.A., 18 Aug. 1980, B. C. Sutton, IMI 252514a.

The epithet '*complex*' commemorates the complications caused for the authors when Dr B. C. Sutton discovered this species less than a day after the original manuscript was submitted. Although conidia of this species are strikingly similar in shape to those of some members of *Arthrobotrys* Cda, examination of type material or original descriptions of all validly published species of *Arthrobotrys* known to us satisfied us that it has not been described previously in that genus. The appearance of conidia of *G. complex* is misleading, however, and the fungus does not belong in *Arthrobotrys*, a genus with sequential conidial development and schizolytic secession. Species of *Arthrobotrys* characteristically trap nematodes and other small animals, whereas this species, like *G. simplex* was found growing on an *Alternaria* species of the '*alternata*' group. Apart from the conidial septation, *G. complex* and *G. simplex* differ only in minor respects: proliferating cells on conidiophores of *G. simplex* tend to be cylindrical, whereas those of *G. complex* often taper slightly like those of *Gonatobotryum fuscum* and *G. parasiticum* (Figs 11, 12); percurrent proliferation is clearly present in *G. complex*, but has yet to be observed in *G. simplex*, and there may be a tendency for separating cells of the two species to break at different points. *Gonatobotrys complex* is known only from the type locality, and one other site about 50 km distant.

* This author's name should be cited thus to avoid confusion with J. C. Walker, an earlier plant author with the same initials.

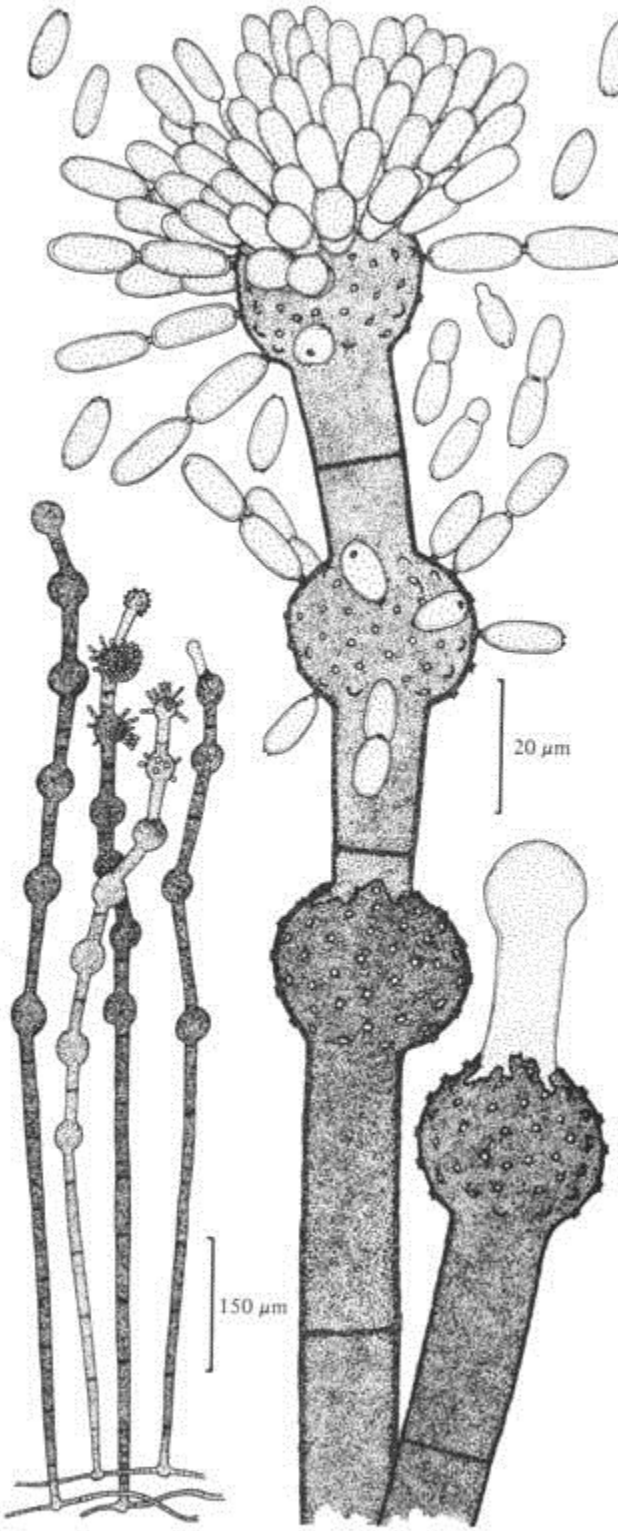


Fig. 11. *Gonatobotryum fuscum*.

GONATOBOTRYUM Sacc., *Michelia* **2**: 24 (1880).

Gonatorrhodiella Thaxt., *Bot. Gaz.* **16**: 202 (1891).
Gonatorhodis Clem., *Gen. Fungi* p. 387 (1931). (Nom. superfl., art. 63.)
Christiaster Kuntze, *Rev. Gen. Pl.* **2**: 848 (1891). (Nom. superfl., art. 63.)

Mycelium hyaline to dark brown, septate, branched, superficial. *Conidiophores* mononematous, macronematous, broad, erect, septate, hyaline to dark brown, smooth or roughened, thin-walled, unbranched or rarely branched. *Conidiogenous cells* terminal, usually becoming intercalary by continuous or percurrent proliferation or by percurrent regeneration, integrated, hyaline to dark brown, smooth or roughened, thin-walled, globose, producing conidia from up to about 100 loci. *Conidia* hyaline to pale brown, aseptate, rarely 1-septate, smooth or roughened, produced in simple chains of 2–3 or in branched chains up to 8 conidia long. *Conidial ontogeny* holoblastic, polyblastic, proximal conidia developing synchronously. *Conidial secession* with separating cells, in at least one species rhexolytic, leaving more or less conspicuous unblackened or blackened denticles on the conidia and conidiogenous cells.

Type species: *Gonatobotryum fuscum* (Sacc.) Sacc.

GONATOBOTRYUM FUSCUM (Sacc.) Sacc., *Michelia* **2**: 24–25 (1880). (Figs 11, 29–34)

Gonatobotrys fusca Sacc., *Michelia* **1**: 84 (1877).
Christiaster fuscus (Sacc.) Kuntze, *Rev. Gen. Pl.* **2**: 848 (1891, as '*fuscens*').

Colonies dark brown. *Conidiophores* light to dark brown, slightly roughened, 250–2000 × 11–16 μm. *Conidiogenous cells* light to dark brown, slightly roughened, with a swollen part 28–38 × 23–38 μm. *Conidia* in simple chains of 2, light brown, slightly roughened, ellipsoid, 10–15 × 5–7 μm, with blackened denticles. The roughening in this species has a reticulate pattern and results from unevenness of the outer wall.

Specimens examined: on rotting wood of *Quercus*, Montello, Treviso, Italy, 1876, Mycotheca Veneta 1090, holotype, K; also IMI 1057, 1674, 6844, 50741.

Shigo (1960) showed that *G. fuscum* is a contact mycoparasite. It has been recorded from bark and wood of various trees including *Fagus* and *Quercus* and as a parasite of a variety of fungi including species of *Ceratocystis*, *Chalaropsis* (Vincent, 1953), *Graphium* and *Leptographium* from Europe (Great Britain, Italy) and North America (U.S.A.: Virginia).

Gonatobotryum parasiticum (Thaxt.) Jane Walker & Minter, comb.nov. (Figs 12, 25–28)

Gonatorrhodiella parasitica Thaxt., *Bot. Gaz.* **16**: 202 (1891).
Nematogonum parasiticum (Thaxt.) Hughes, *Can. J. Bot.* **31**: 593 (1953).
Gonatorhodis parasitica (Thaxt.) Clem., *Gen. Fungi*: 387 (1931).
Gonatorrhodiella eximia Höhn., *Sber. Akad. Wiss. Wien*, Abt. I, **116**: 146–147 (1907).
Gonatobotrys lateritia Peck, *Bull. N.Y. St. Mus.* **131**: 21–22 (1909).

Colonies white, becoming orange. *Conidiophores* hyaline to pale brown, smooth, 250–2000 × 9–15 μm. *Conidiogenous cells* hyaline to pale brown, smooth, with a swollen part 28–38 × 24–45 μm. *Conidia* in simple chains of 3, hyaline to pale brown, smooth or slightly roughened, elliptical, 5–12 × 4–7 μm, with unblackened inconspicuous denticles.

Specimens examined: on decaying *Hypocrea*, West Haven, Conn., U.S.A., 10 Oct. 1888, R. Thaxter, holotype of *Gonatorrhodiella parasitica*, FH 516; on *Tremella lutescens*, Wiener Wald, Austria, 23 July 1906, F. Höhnel, Höhn. herb. no. 433, holotype of *Gonatorrhodiella eximia*, FH; on decaying *Poria*, Star Lake, N.Y., U.S.A., 10 Aug. 1907, C. Peck, holotype of *Gonatobotrys lateritia*, NYS; *Gonatorrhodiella parasitica* on *Polyporus betulinus*, 1905, ex herb. Farlow, K; IMI 208296.

This species is parasitic on other fungi (Ayers, 1941; Davidson, 1935). The mode of parasitism remains unspecified, but in view of the similarity of this species to *G. fuscum*, it is likely that this species too will be a contact mycoparasite. *Gonatobotryum parasiticum* has been recorded from *Ganoderma*, *Hypocrea*, *Hypomyces*, *Polyporus*, *Poria*, *Tremella* and *Trichoderma* from Europe (Austria) and North America (U.S.A.: Connecticut, New York). The records suggest that *G. parasiticum* parasitizes members of the Hypocreaceae themselves growing on other decaying fungi.

GONATOBOTRYUM APICULATUM (Peck) Hughes, *Can. J. Bot.* **31**: 593 (1953). (Figs 13, 35–42)
Haplographium apiculatum Peck, *Bull. N.Y. St. Mus.* **28**: 62 (1875).

Colonies dark brown. *Conidiophores* light to dark brown, often roughened towards the base, otherwise smooth, 250–1500 × 5–12 μm. *Conidiogenous cells* light to dark brown, smooth, with a swollen part 10–24 × 7–19 μm. *Conidia* in branched chains up to 8 long, distal conidia being smaller than the proximal ones, light brown, smooth, elliptical to

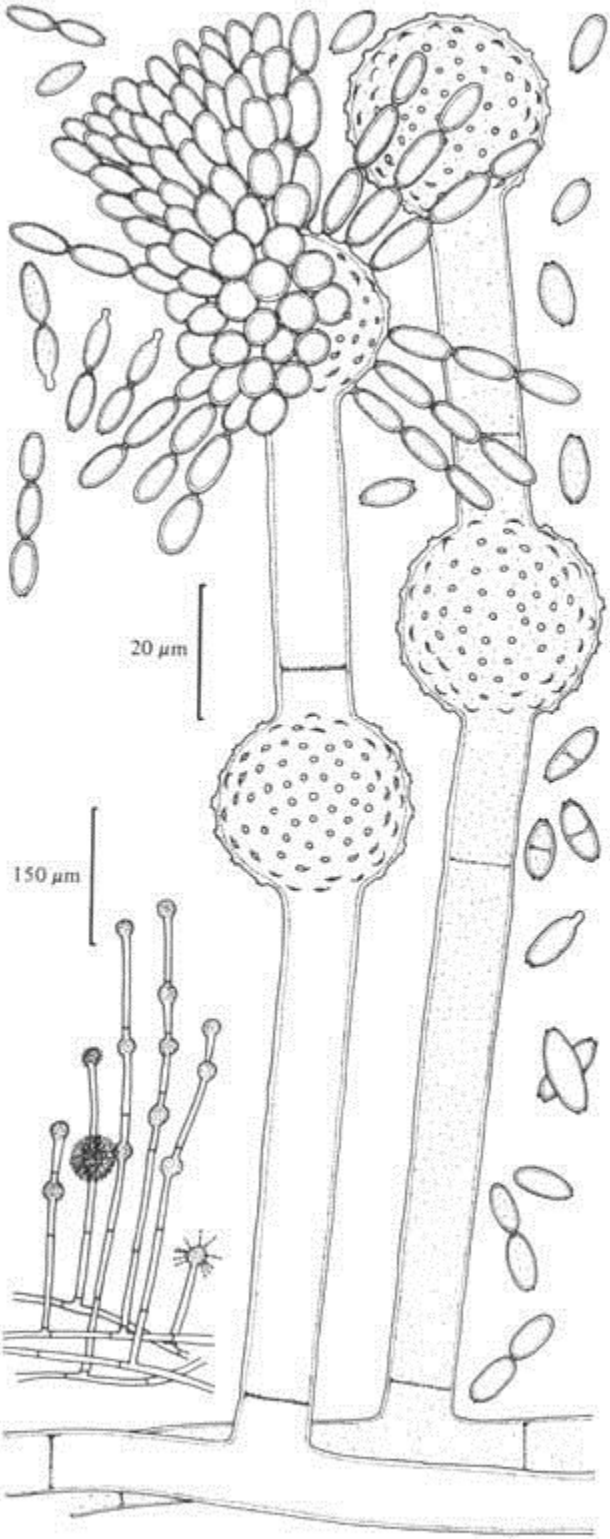


Fig. 12. *Gonatobotryum parasiticum.*

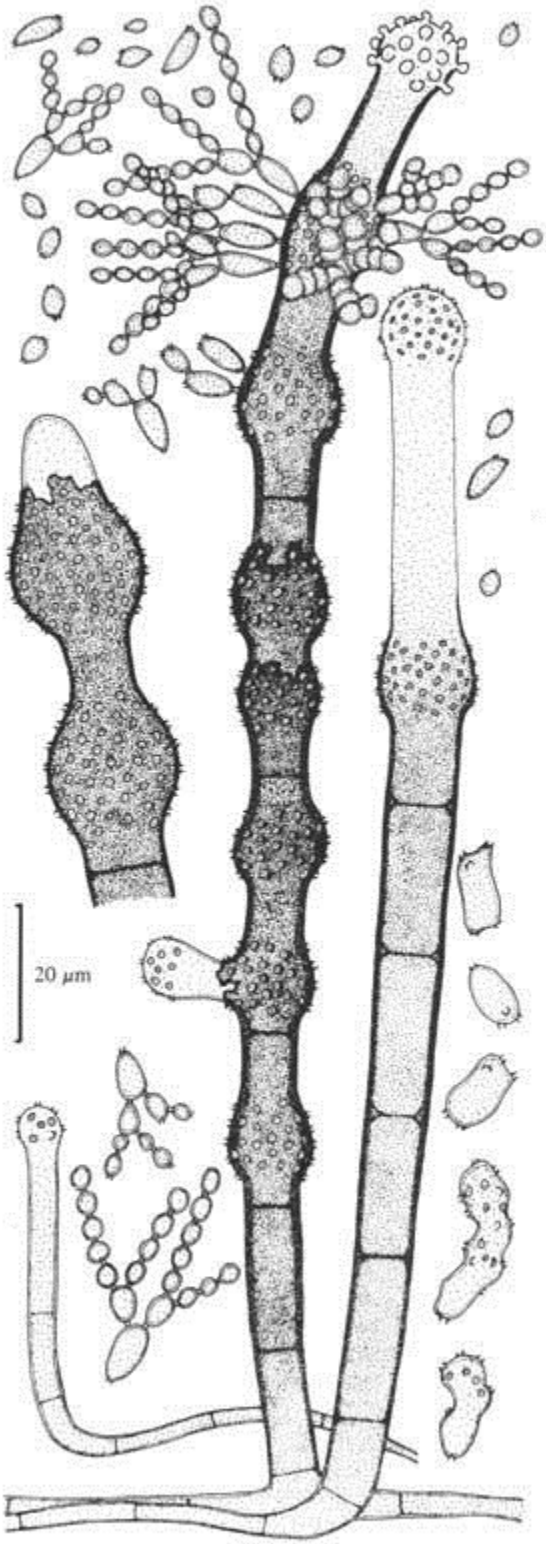


Fig. 13. *Gonatobotryum apiculatum.*

globose, 3–13 × 2–7 μm, with conspicuous unblackened denticles, rhexolytic.

Specimens examined: on galls of *Brysocrypta hamamelidis* on *Hamamelis*, Bethlehem, N.Y., U.S.A., C. Peck, holotype, NYS; also IMI 110033, 131792, 171081.

In most specimens of this species conidia bearing more than three branches are rare, and these branches almost invariably arise from the apical part of the conidium. In one specimen examined (IMI 110033), however, some conidia were observed with up to 18 denticles, not restricted to the apical region of the conidium, providing evidence of a rather different branching pattern. This specimen might be worthy of varietal status. The roughening on the lower parts of some conidiophores of this species has a circular pattern, the circles having tattered edges, with the appearance of minute burst blisters, very different from the roughening in *G. fuscum*. Similar roughening has been observed on conidiophores of *Acrophialophora* J. C. Edward. Although the conidial ontogeny and secession of this species have been extensively studied (Cole, 1973; Kendrick *et al.*, 1968), we know of no instance where it has been associated with other fungi. In the discussion above, it was observed that this species is probably not related phylogenetically to *G. fuscum* and *G. parasiticum*. It is quite possible therefore that *G. apiculatum* is not a contact mycoparasite. *Gonatobotryum apiculatum* has been recorded from *Anacardium*, *Hamamelis*, *Rhus* and soil of *Pinus* from Asia (India) and North America (Canada, U.S.A.: New York).

EXCLUDED TAXA

DICELLISPORA LELEBAE Sawada, *Rep. Govt. Res. Inst. Dep. Agric. Formosa* **87**: 74 (1944). (Nom. inval., art. 36.)

Kendrick & Carmichael (1973) treated *Dicellispora* as a synonym of *Gonatobotryum*.

GONATOBOTRYS AFRICANA Saccas, *Agron. trop. Nogent* **9**: 40 (1954).

Judging from the original description and illustration, this fungus is probably a species of *Olpitrichum* Atk.

GONATOBOTRYS BLIGHIAE Frag. & Cif., *Estac. Agron. Moca Fer. Bot.* **11**: 59 (1928).

The dimensions given in the original description, particularly the narrowness of the conidiophores are incompatible with *Gonatobotrys* as circumscribed here. We have been unable to place this fungus satisfactorily elsewhere.

GONATOBOTRYS FLAVA Bonord., *Handb. Mykol.*: 105 (1851).

Bonorden's collections of this species (herb. G) were examined, but no fungus similar to his description could be found. Although it is difficult to be certain, judging by the original illustration, *G. flava* is probably a synonym of *Nematogonum ferrugineum*.

GONATOBOTRYS HETEROSPORA Peyr., *Nuovo G. bot. ital.* **25**: 454 (1920).

Judging from the original description and illustration, this fungus is probably a species of *Acladium* Link.

GONATOBOTRYS MACULICOLA Winter, *Hedwigia* **22**: 1 (1883).

Gonatobotryum maculicola (Winter) Sacc., *Syll. Fung.* **4**: 278 (1886, as '*maculicolum*').

Christiaster maculicola (Winter) Kuntze, *Rev. Gen. Pl.* **2**: 848 (1891, as '*maculicolus*').

There is no extant collection of this species in Winter's herbarium in B. The type is thus apparently lost and *G. maculicola* is probably best regarded as a nomen dubium.

GONATOBOTRYS MICROSPORA Riv., *Parassiti*: 490 (1884).

Cunninghamella microspora (Riv.) Matruchot, *Annls mycol.* **1**: 56 (1903).

Cunninghamella microspora is, fide Drechsler (1950), the correct disposition of Rivolta's (1884) species.

GONATOBOTRYS PALLIDULA Bres., *Annls mycol.* **1**: 127 (1903).

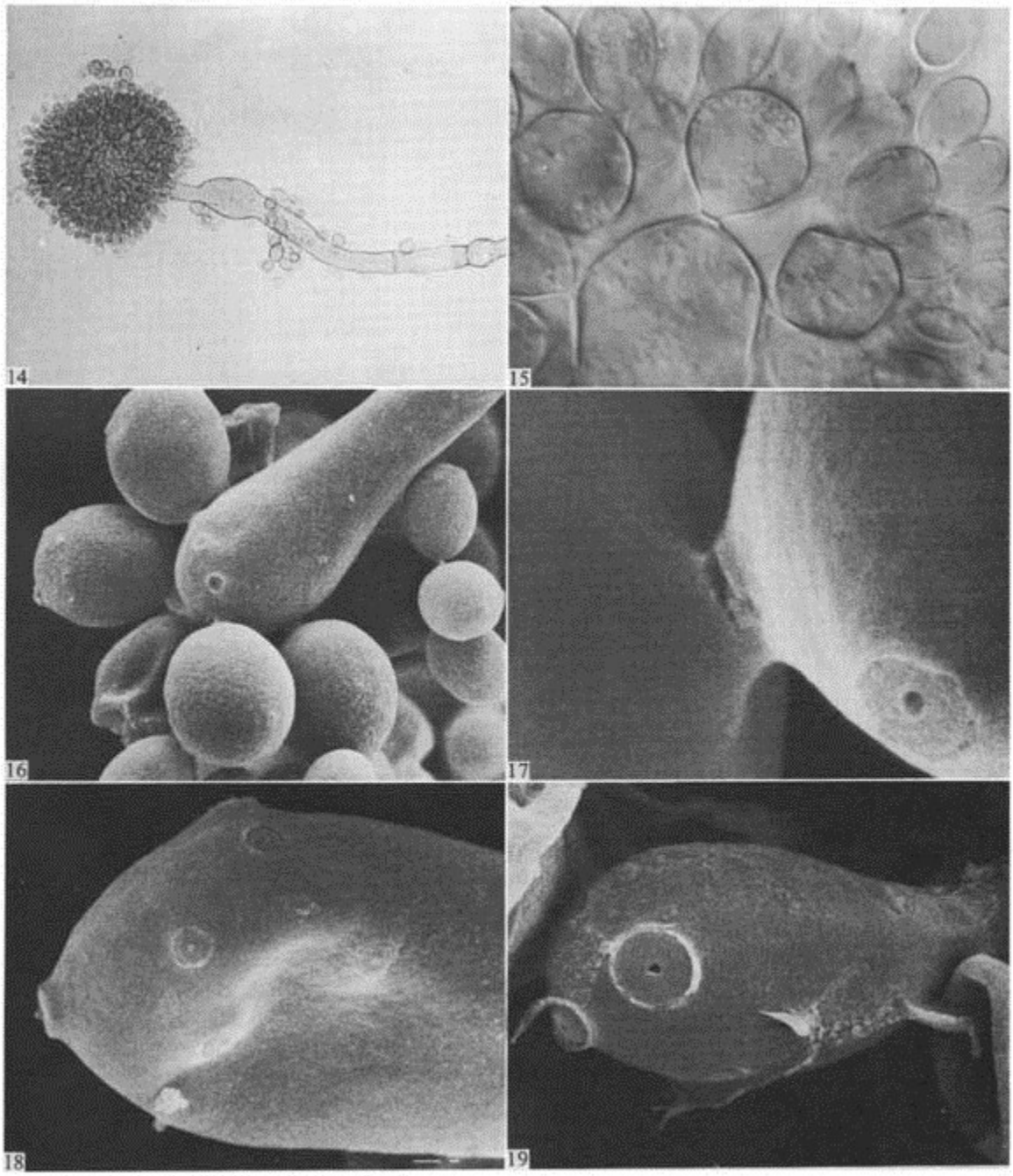
Peniophora pallidula (Bres.) Bres. apud Bourdot & Galzin, *Bull. trimest. Soc. mycol. Fr.* **28**: 390 (1912).

Hyphodontia pallidula (Bres.) John Eriksson, *Symb. bot. upsaliens.* **16**: 104 (1958).

Hyphodontia pallidula is, fide Eriksson (1958), the correct disposition of this species.

GONATOBOTRYS RAMOSA Riess apud Fresenius, *Beitr. Mykol.*: 44 (1863).

We have been unable to trace the type of this species and the original description and illustration are inadequate. Coemans' (1863) illustration of this species is reminiscent of *Nematogonum ferrugineum*, but it is probably best regarded as a nomen dubium.



Figs. 14–19. *Nematogonum ferrugineum.*

Fig. 14. Conidiophore with terminal conidiogenous cell bearing chains of conidia (× 150).

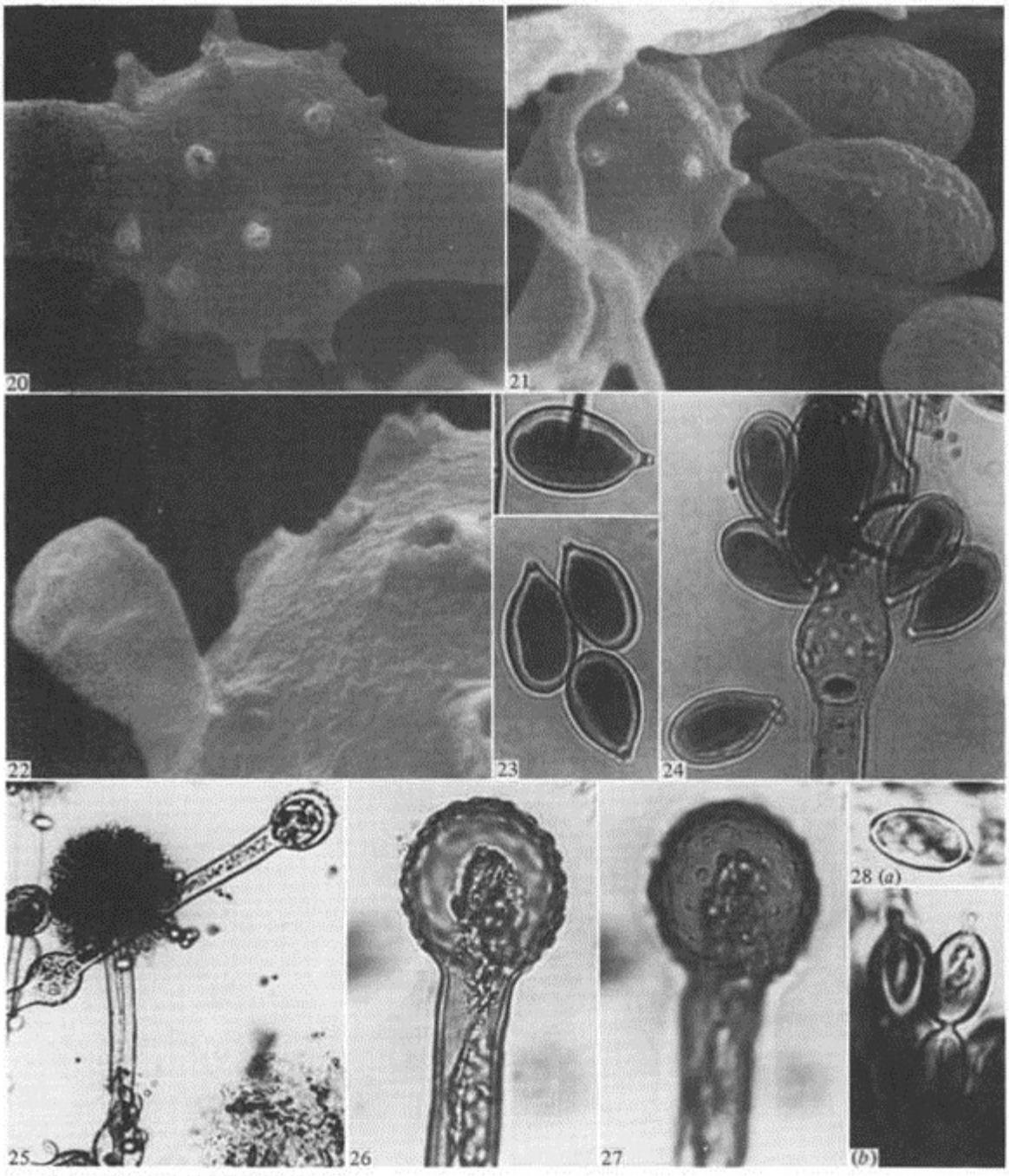
Fig. 15. Conidium delimited from conidiogenous cell by a single septum (× 1000).

Fig. 16. SEM. Scars from seceded conidia visible on conidiogenous cell bearing proximal conidia (× 1450).

Fig. 17. SEM. Conidium at point of secession (× 13750).

Fig. 18. SEM. Scars on a conidiogenous cell (× 2750).

Fig. 19. SEM. Scars on a conidium (× 3850).



Figs. 20–24. *Gonatobotrys simplex*.

Fig. 20. SEM. Intercalary conidiogenous cell with conspicuous denticles (×4000).

Fig. 21. SEM. Conidia and intercalary conidiogenous cell (×2500).

Fig. 22. SEM. Aborted conidium on older conidiogenous cell bearing less conspicuous denticles (×10000).

Fig. 23. Conidia with conspicuous denticles (×1500).

Fig. 24. Intercalary conidiogenous cell with conidia (×1500).

GONATOBOTRYS RAMOSISSIMA Arnaud, *Bull. trimest. Soc. mycol. Fr.* **68**: 187 (1952). (Nom. inval., art. 36.)

Sporothrix ramosissima Arnaud ex de Hoog, *CBS Studies in Mycology* **7**: 28 (1974).

GONATOBOTRYUM BAHIENSE Batista, *Anais Soc. Biol. Pernamb.* **13**: 154 (1955).

The dimensions given in the original description, particularly the narrowness of the conidiophores are incompatible with *Gonatobotryum* as circumscribed here. We have been unable to obtain the type specimen and cannot place this fungus satisfactorily elsewhere.

GONATOBOTRYUM DICHOTOMUM Cooke & Massee, *Grevillea* **16**: 15 (1887).

The holotype in K is in poor condition and the original description is inadequate. *Gonatobotryum dichotomum* is thus probably best regarded as a nomen dubium.

GONATOBOTRYUM INDICUM Munjal & Gill, *Indian Phytopath.* **16**: 62 (1963).

This species was described from India on twigs in association with a *Sporidesmium* sp. Part of the holotype (HCIO 27078) has been examined, but no fungus corresponding to the original description and illustration could be found. *Gonatobotryum indicum* may, to judge from the original description and illustration, be a synonym of *Gonatobotryum fuscum*.

GONATOBOTRYUM SCLEROTIGENUM van Warmelo, *Bothalia* **10**: 347 (1971).

The holotype of this species (PRE 44252) has been examined. The conidia appear to secede by schizolysis, and this combined with the presence of sclerotia suggests strongly that the taxon belongs in *Botrytis* Mich. ex Pers.

GONATOBOTRYUM TENELLUM (Peck) Peck, *Bull. N.Y. St. Mus.* **131**: 104 (1909).

Spondylocladium tenellum Peck, *Bull. N.Y. St. Mus.* **32**: 41 (1879).

Although we have not seen the type material, Peck's description of the spores being produced in verticils of 2–4 at the septa of the conidiophores suggests that this species belongs in none of the three genera recognized here. We have been unable to place it satisfactorily elsewhere.

GONATORRHODIELLA COCCORUM Petch, *Trans. Br. mycol. Soc.* **10**: 181 (1925).

The holotype in K is in poor condition, but it is obvious that this species does not belong in *Gonatobotryum*, *Gonatobotrys* or *Nematogonum*. Petch himself doubted whether it was correctly placed in *Gonatorrhodiella*. The fungus is entomogenous, with very narrow conidiophores (1·5–2 μm wide), and to judge from the illustration by Petch the conidia are probably produced phialidically. Samson *et al.* (1980) have recently described a new genus, *Pleurodesmospora*, for this species.

GONATORRHODUM CLERODENDRI Chona & Munjal, *Indian Phytopath.* **9**: 62 (1956).

Part of the holotype (from HCIO) has been examined and no fungus corresponding to the original description and illustration could be found. Although the general dimensions are consistent with the three genera recognized here, *Gonatorrhodum clerodendri* was described as having conidia with verrucose walls, 2 μm thick, produced in basipetal chains, which is suggestive of *Periconia* Tode ex Fr.

GONATORRHODUM FUSCUM Pr., *Linnaea* **24**: 122 (1851).

The holotype (in B) has recently been examined and was found to contain a species of *Cladosporium* Link ex Fr. (Holubová, pers. comm.).

GONATORRHODUM SPECIOSUM Cda, *Pracht-fl.*: 5 (1839).

Corda's collections of this species are not preserved in PRM. It thus seems certain that the type material is lost. In the past *Gonatorrhodum* has been regarded as a possible earlier name for *Gonatobotryum* (Kendrick & Carmichael, 1973) since it was described by Corda as producing branched chains of conidia from swollen nodes on the conidiophores. Corda however illustrated the ramoconidia of these branched chains as being septate, a feature rarely seen in species accepted

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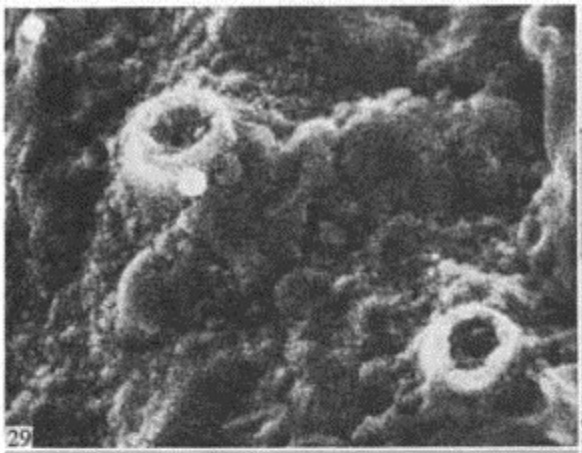
Figs. 25–28. *Gonatobotryum parasiticum*.

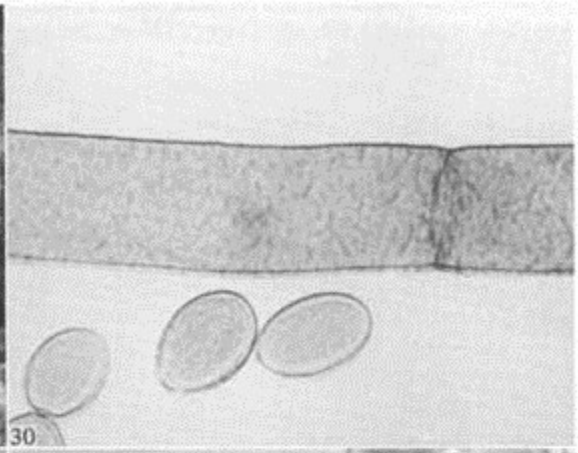
Fig. 25. Terminal conidiogenous cell bearing conidia; intercalary and terminal conidiogenous cells with no conidia, ex holotype (× 350).

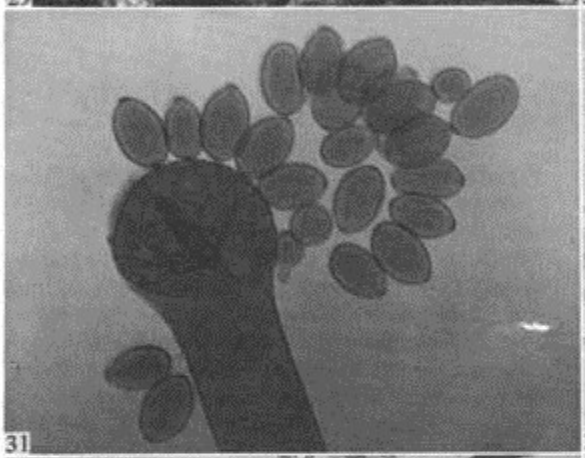
Fig. 26. Conidiogenous cell focused to show denticles in side view (× 900).

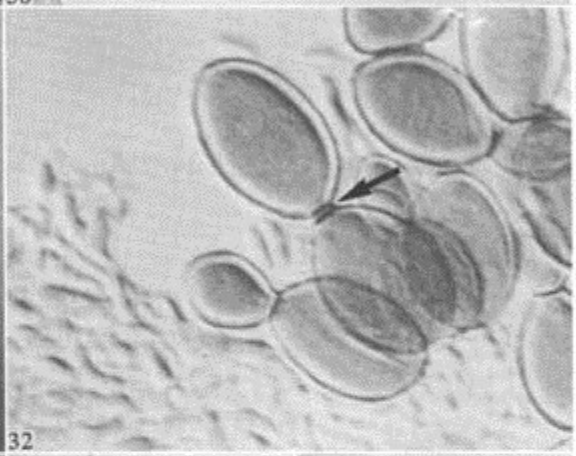
Fig. 27. The same conidiogenous cell with denticles in surface view (× 900).

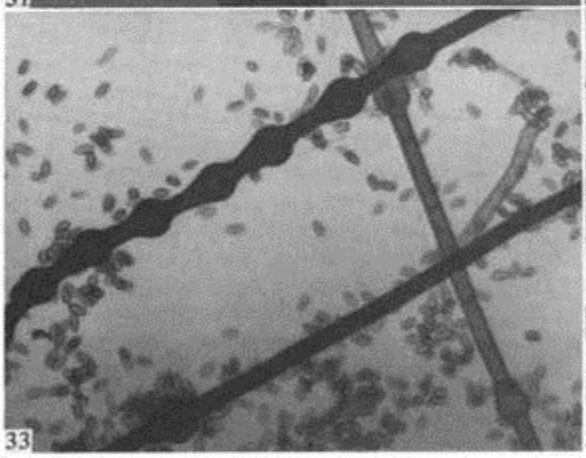
Fig. 28. Seceded conidium with small denticle and developing chain of three conidia (× 1300).

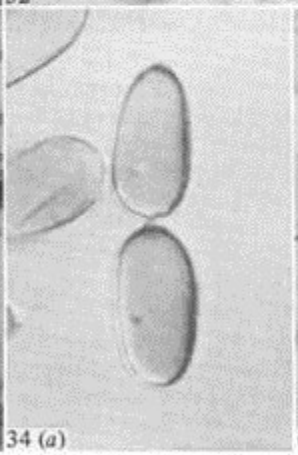


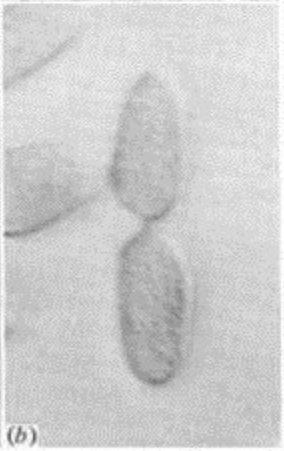












Figs. 29–34. *Gonatobotryum fuscum*.

Fig. 29. SEM. Denticles on a conidiogenous cell (× 12000).

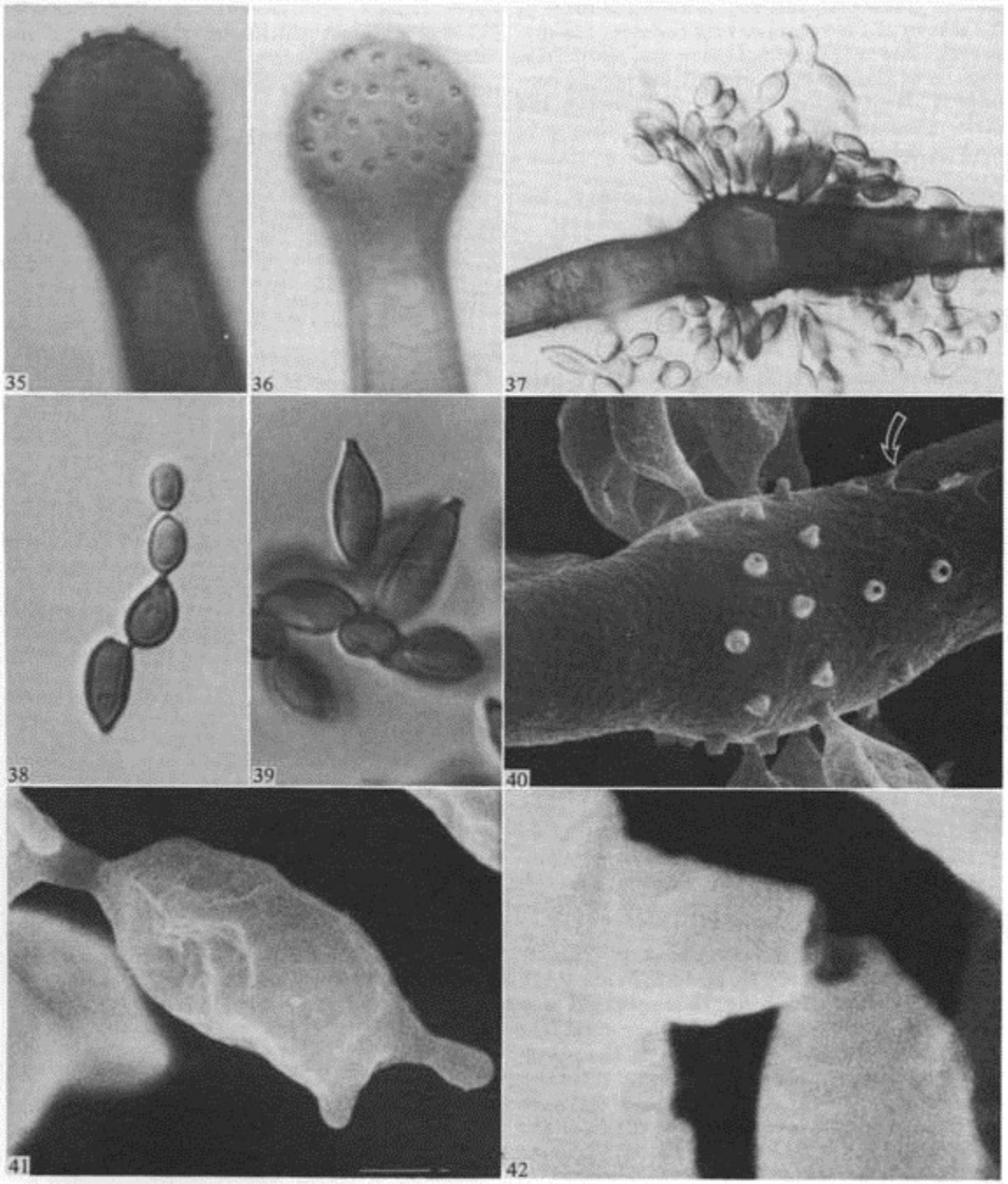
Fig. 30. Reticulate roughening of conidiophore wall (× 1000).

Fig. 31. Small separating cells between conidia and conidiogenous cell, small denticles on both after secession (× 700).

Fig. 32. Single black lines delimiting developing conidia; two black lines delimiting mature conidia (arrow). Ascospores of a parasitized *Ceratocystis* are also visible (× 1630).

Fig. 33. Variation in the frequency of conidiogenous cells and the density of pigmentation (× 160).

Fig. 34. A chain of two mature conidia (a), refocused to show slightly roughened surface (b) (× 1550).



Figs. 35–42. *Gonatobotryum apiculatum*.

Fig. 35. Conidiogenous cell focused to show denticles in side view (× 1500).

Fig. 36. The same conidiogenous cell with denticles in surface view (× 1500).

Fig. 37. Conidia and separating cells on an intercalary conidiogenous cell (× 1000).

Fig. 38. A chain of conidia with conspicuous separating cells (× 1600).

Fig. 39. Denticles on seceded conidia (× 1750).

Fig. 40. SEM. Conidia and denticles on an intercalary conidiogenous cell. Percurrent proliferation is arrowed (× 3000).

Fig. 41. SEM. Proximal conidium with the initials of two branches (× 9500).

Fig. 42. SEM. Denticles of recently seceded conidium and conidiogenous cell (× 30000).

here in *Gonatobotryum*, and reminiscent more of the species of *Cladosporium* with nodulose conidiophores. The original description and illustration seem to us inadequate to identify the species confidently. We therefore consider *G. speciosum* and hence *Gonatorrhodum*, the genus it typifies, to be nomina dubia.

NEMATOGONUM ALBUM Bainier, *Bull. trimest. Soc. mycol. Fr.* **21**: 227–228 (1905).

A synonym of *Oidium candidans* (Sacc.) Linder, fide Linder (1942).

NEMATOGONUM BYSSINUM Ces., *Bot. Ztg* **11**: 238 (1853).

Cesati's description is meagre, we have been unable to trace the type specimen, Saccardo (1886) considered this a very doubtful species.

NEMATOGONUM FUMOSUM Bonord., *Handb. Mykol.*: 116 (1851).

A synonym of *Syzygites megalocarpus* Ehrenb. ex Fr., fide Hesseltine (1957).

NEMATOGONUM HUMICOLA Oudem., *Archs néerl. Sci.* II, **7**: 274 (1902).

The dimensions given in the original description, particularly the narrowness of the conidiophores, are incompatible with *Nematogonum* as circumscribed here. The type specimen could not be traced at L and we cannot place this fungus satisfactorily elsewhere.

NEMATOGONUM SIMPLEX Bonord., *Handb. Mykol.*: 117 (1851).

A synonym of *Syzygites megalocarpus* fide Hesseltine (1957).

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REFERENCES

ALI, M. I. (1975). The family Moniliaceae in Egypt. 1. *Gonatobotrys simplex* Corda. *Publications from Cairo University Herbarium* **6**, 1–6.

AYERS, T. T. (1941). The distribution and association of *Gonatorrhodiella highlei* with *Nectria coccinea* in the United States. *Mycologia* **33**, 178–187.

BAINIER, M. G. (1880). *Sterigmatocystis* et *Nematogonum*. *Bulletin, Société Botanique de France* **27**, 27–33.

BAINIER, M. G. (1907). Mycothèque de l'Ecole de Pharmacie: XIX. *Bulletin de la Société Mycologique de France* **23**, 128–131.

BARNETT, H. L. (1958). A new *Calcarisporium* parasitic on other fungi. *Mycologia* **50**, 497–500.

BARNETT, H. L. & BINDER, F. L. (1973). The fungal host–parasite relationship. *Annual Review of Phytopathology* **11**, 273–292.

BLYTH, W. (1949). Studies on *Gonatorrhodiella highlei* A. L. Smith. *Transactions and Proceedings of the Botanical Society of Edinburgh* **35**, 157–179.

BOOTH, C. (1977). *Nectria coccinea*, *Nectria coccinea* var. *faginata*. *C.M.I. Descriptions of pathogenic fungi and bacteria*, nos. 532, 533. Commonwealth Mycological Institute.

BUTLER, E. E. & MCCAIN, A. H. (1968). A new species of *Stephanoma*. *Mycologia* **60**, 955–959.

COEMANS, E. (1863). Révision de generes *Gonatobotrys* et *Arthrobotrys* Corda. *Bulletin de la Société Royale de Botanique de Belgique* **2**, 167–178.

COLE, G. T. (1973). Ultrastructural aspects of conidiogenesis in *Gonatobotryum apiculatum*. *Canadian Journal of Botany* **51**, 1677–1684.

COLE, G. T. & SAMSON, R. A. (1979). *Patterns of Development in Conidial Fungi*. London, San Francisco, Melbourne: Pitman Publishing Ltd.

COOKE, B. E. (1974). The development of conidiophores and conidia in the imperfect fungus *Oedocephalum roseum*. *New Phytologist* **73**, 115–130.

DAVIDSON, R. W. (1935). Forest pathology notes. *Plant Disease Reporter* **19**, 94–97.

DRECHSLER, C. (1950). Several species of *Dactylella* and *Dactylaria* that capture free-living nematodes. *Mycologia* **42**, 1–79.

EHRLICH, J. (1942). Occurrence of *Gonatorrhodiella highlei* in Nova Scotia and New Brunswick. *Mycologia* **34**, 705.

ERIKSSON, J. (1958). Studies in the Heterobasidiomycetes and Homobasidiomycetes – Aphyllophorales of Muddus National Park in North Sweden. *Symbolae Botanicae Upsalienses* **16**, 1–172.

GAIN, R. E. & BARNETT, H. L. (1970). Parasitism and axenic growth of the mycoparasite *Gonatorrhodiella highlei*. *Mycologia* **62**, 1122–1129.

GAMS, W. (1975). *Nematogonium niveum*, a new hyperparasitic species of hyphomycetes. *Revue de Mycologie* **39**, 273–278.

HARZ, C. O. (1871). Einige neue Hyphomyceten Berlin's und Wien's nebst Beiträgen zur systematic derselben. *Bulletin de la Société Imperiale des Naturalistes de Moscou* **44**, 88–147.

HESSELTINE, C. W. (1957). The genus *Syzygites* (Mucoraceae). *Lloydia* **20**, 228–237.

HOCH, H. C. (1977). Mycoparasitic relationships: *Gonatobotrys simplex* parasitic on *Alternaria tenuis*. *Phytopathology* **67**, 309–314.

HOCH, H. C. (1978). Mycoparasitic relationships. IV. *Stephanoma phaeospora* parasitic on a species of *Fusarium*. *Mycologia* **70**, 370–379.

HOOG, G. S. DE (1974). The genera *Blastobotrys*, *Sporothrix*, *Calcarisporium* and *Calcarisporiella* gen.nov. *Studies in Mycology* no. 7. Centraalbureau voor Schimmelcultures.

HUGHES, S. J. (1953). Conidiophores, conidia and classification. *Canadian Journal of Botany* **31**, 577–659.

HUGHES, S. J. (1979). Relocation of species of *Endophragmia* auct. with notes on relevant generic names. *New Zealand Journal of Botany* **17**, 139–188.

KENDRICK, W. B. (1980). The generic concept in hyphomycetes – a reappraisal. *Mycotaxon* **11**, 339–364.

KENDRICK, W. B. & CARMICHAEL, J. W. (1973). Hyphomycetes. In *The Fungi*, vol. 4A (ed. G. C. Ainsworth, F. K. Sparrow & A. S. Sussman), pp. 323–509. New York, London: Academic Press.

KENDRICK, W. B., COLE, G. T. & BHATT, G. C. (1968). Conidium ontogeny in hyphomycetes. *Gonatobotryum apiculatum* and its botryose blastospores. *Canadian Journal of Botany* **46**, 591–596.

LINDER, D. H. (1942). A contribution towards a monograph of the genus *Oidium* (Fungi Imperfecti). *Lloydia* **5**, 165–207.

MADELIN, M. F. (1979). An appraisal of the taxonomic significance of some different modes of producing blastic conidia. In *The Whole Fungus*, vol. 1 (ed. W. B. Kendrick), pp. 63–80. Ottawa: National Museum of Natural Sciences, National Museums of Canada and the Kananaskis Foundation.

MARVANOVÁ, L. (1977). A contact biotrophic mycoparasite on aquatic hyphomycete conidia. *Transactions of the British Mycological Society* **68**, 485–488.

MATRUCHOT, L. (1892). *Recherches sur le Développement de Quelques Mucédinées*. Paris: Armand Colin.

MATSUSHIMA, T. (1975). *Icones Microfungorum a Matsushima Lectorum*. Published by the author, Kobe, Japan.

PERRIN, R. (1977). *Gonatorrhodiella highlei* A. L. Smith, hyperparasite de *Nectria coccinea* Pers. ex Fries, un des agents de la maladie du hetre. *Compte rendu hebdomadaire des séances de l'Académie d'agriculture de France* **63**, 67–70.

PERRIN, R. (1979). Menace sur les hetres. *Recherche* **10**, 1275–1276.

PERSOON, C. H. (1822). *Mycologia Europaea*. Erlangen.

SACCARDO, P. A. (1886). *Sylloge Fungorum*, vol. 4. Pavia: P. A. Saccardo.

SAMSON, R. A., GAMS, W. & EVANS, H. C. (1980). *Pleurodesmospora*, a new genus for the entomogenous hyphomycete *Gonatorrhodiella coccorum*. *Persoonia* **11**, 65–69.

SHIGO, A. L. (1960). Parasitism of *Gonatobotrym fuscum* on species of *Ceratocystis*. *Mycologia* **52**, 584–598.

STALPERS, J. A. (1974). Revision of the genus *Oedocephalum* (Fungi Imperfecti). *Proceedings. Koninklijke Nederlandse Akademie van Wetenschappen, Series C*, **77**, 383–401.

SUTTON, B. C. (1973). Hyphomycetes from Manitoba and Saskatchewan, Canada. *Mycological Papers* **132**, 1–143. Commonwealth Mycological Institute.

RIVOLTA, S. (1884). *Dei parassiti vegetali, come introduzione allo studio delle malattie parassitarie e delle alterazioni dell'alimento degli animali domestici*, 2nd ed., pp. 592, Torino.

VINCENT, M. (1953). A *Chalaropsis* on beech. *Nature, London* **172**, 963.

VUILLEMIN, M. P. (1911). Repartition des Gonatobotrytideae entre les Conidiosporés et les Blastosporés. *Bulletin, Société Botanique de France* **58**, 164–170.

WHALEY, J. W. & BARNETT, H. L. (1963). Parasitism and nutrition of *Gonatobotrys simplex*. *Mycologia* **55**, 199–210.

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