Revision of predacious Hyphomycetes in the *Dactylella-Monacrosporium* complex

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1 Abstract

Nematophagous hyphomycete species described in the anamorph-genera *Dactylella* Grove 1884, *Monacrosporium* Oudem. 1885, and allied genera are revised. These include most of the known predacious species that form trapping organs enabling them to capture nematodes and other microscopic animals, with the exception of *Arthrobotrys* Corda.

The revision is mainly based on isolates kept in the Centraalbureau voor Schimmelcultures, Baarn, and about 180 of my own isolates. Preserved material was only studied as far as type specimens were concerned. Emphasis is laid on morphological characters, especially on conidium and conidiophore morphology and the type of trapping organ. In addition, a few physiological-biochemical characters were assessed in order to clarify the specific and generic delimitation.

Dactylella is typified by *D. minuta* which is, as far as we know, a non-nematophagous species. The genus should, therefore, be reserved for non-predacious species. The large group of nematode-trapping hyphomycetes are retained in (or newly transferred to) the two genera *Arthrobotrys* and *Monacrosporium*. For practical reasons these two genera are kept distinct, though they are believed to be closely related. Their phylogeny is discussed.

Drechsleromyces Subram. and *Gangliophragma* Subram. are regarded as synonyms of *Dactylella*. *Drechslerella* Subram., *Golovinia* Mekht., *Monacrosporiella* Subram., and *Kafiaddinia* Mekht. are synonymised with *Monacrosporium*, *Dactylariopsis* Mekht., *Geniculifera* Rifai, *Nematophagus* Mekht., and *Woroninula* Mekht. with *Arthrobotrys*.

Thirty-nine species are accepted in *Monacrosporium*. All these species are described and illustrated. A teleomorph connection is reported for the first time for a species of *Monacrosporium*. A dichotomous key for the predacious species, primarily based on the morphology of trapping organs, is presented. A checklist of all specific epithets used in this complex (including excluded species) is provided.

The following new combinations are proposed: *Arthrobotrys nematopaga* (Mekht. & Faisieva) A. Rubner, *Dactylella cylindrospora* (R.C. Cooke) A. Rubner, *Monacrosporium arcuatum* (Scheuer & Webster) A. Rubner, *M. asthenopagum* (Drechsler) A. Rubner, *M. copepodii* (G.L. Barron) A. Rubner, *M. iridis* (Ts. Watan.) A. Rubner & W. Gams, *M. leptosporum* (Drechsler) A. Rubner, *M. lobatum* (Dudd.) A. Rubner, *M. multiforme* (Dowsett, J. Reid & Kalkat) A. Rubner; *M. tentaculatum* A. Rubner & W. Gams nom. nov. replaces *Laridospora appendiculata* (Anastasiou) Nawawi. [p. 2]

2 Introduction

This study has arisen from ecological work with nematode-trapping hyphomycetes, and this fact partly explains a certain bias in the present revision to the predacious rather than non-predacious fungi of the *Dactylella-Monacrosporium* complex. In the first phase of this study a large number of nematophagous fungi were isolated and their habitats or substrata were studied. These isolates, together with the strains available in culture collections, formed the basis of the present taxonomical investigation.

The group of predacious, mostly nematode-trapping fungi is usually sharply delimited morphologically and ecologically from endoparasitic nematophagous fungi. Predacious hyphomycetes (facultatively) capture microscopic animals, such as nematodes, rhizopods, copepods, rotifers, or springtails, by means of specialized hyphal sections (simple mycelial parts with adhesive or strangulating traps). In contrast, endoparasites infect their hosts from germinating spores, developing their thallus inside the infected animal. In the nematophagous hyphomycete genus *Nematoctonus*, anamorphs of the basidiomycete *Hohenbuehelia*, this distinction is impracticable since both modes of life are intimately associated. If traps develop on germinating conidia of predacious fungi, the developing fungus at first also functions as an endoparasite (Saxena *et al.*, 1995).

Among the phragmosporous, hyaline, blastoconidial hyphomycetes, the predacious taxa form a more or less homogeneous group characterized by trapping organs and long erect conidiophores bearing one or more conidia in a sympodial sequence. But several non-predacious taxa are similar and have often been classified in the same genera as predacious species. During this study it became clear that several non-predacious species are morphologically very close to predacious species. Thus, both groups would need a contiguous revision.

Much more fungal material is available of predacious species than of the non-predacious group. Since the discovery of predacious activity in *Arthrobotrys oligospora* (Zopf, 1888), the nematode-trapping fungi have attracted much interest amongst mycologists. The reasons may lie in the spectacular trapping method, in the physiology involved with it and, last but not least, in their potential economic importance as biocontrol agents. Charles Drechsler (1892-1986) devoted a great part of his scientific activities to nematode-trapping fungi (without neglecting the related non-nematophagous species) and laid the foundation of our knowledge of the diversity and taxonomy of this group. His descriptions (until 1945) have been collated by Dollfus (1946) and a key to the described species was published by Cooke and Godfrey (1964).

In contrast, the non-predacious species of the *Dactylella-Monacrosporium* complex have not received much attention and the material available is very limited. The information on *Dactylella* is still poor. Only some of the

species were studied, as documented in the check-list of epithets.

2.1 Historical survey of the generic classification

Many generic names have been applied to fungi capturing nematodes and other microscopic animals. A brief outline of the generic classification is given here. For a detailed survey see Chapter 7. [p. 3]

Dactylium
The first nematophagous species described - without knowing about its potentially predacious activities - was possibly *Dactylium candidum* Nees von Eesenbeck (1817). This species was known for a long time as *Dactylaria candida* (Nees : Fr.) Sacc. (1886). Authors like Barron (1968) declared its identity as doubtful. A nematophagous fungus matching the diagnosis was described in detail by Drechsler (1937), and this species was later also transferred to several other genera.

Dactylium candidum, being the type species of *Dactylium* Nees : Fr., raises nomenclatural problems. The identity of the species cannot be verified since no type material is available. If it were neotypified (with a predacious fungus), *Dactylium* would have to replace *Monacrosporium*. Therefore, and because of the uncertain application, Gams & Rubner (1996) proposed rejection of *Dactylium candidum* (with all later obligate synonyms, such as *Monacrosporium candidum* (Nees : Fr.) Xing-Z. Liu & K.-Q. Zhang) under Art. 56. In this revision '*M. candidum*' sensu Drechsler is replaced by a taxonomic synonym, *M. haptotylum* (Drechsler) Xing-Z. Liu & K.-Q. Zhang.

Arthrobotrys
Corda (1839) described *Arthrobotrys* with *A. superba* as the type species, unaware of its facultative predatory activities. The most common and best investigated species among predacious fungi, *A. oligospora*, was described by Fresenius (1852).

The first taxonomical survey of *Arthrobotrys* was written by Haard (1968). Jarowaja (1970) monographed 25 species. Van Oorschot (1985) recognized 28 species of *Arthrobotrys*. Schenck *et al.* (1977) expanded the genus, recognizing 47 species, as discussed below.

Dactylaria and *Dactylella*
Since the 1930's, many species of the nematode-trapping fungi have been described and classified in *Arthrobotrys*, *Dactylaria*, and *Dactylella*. Most of these taxa were introduced by Drechsler. For almost 40 years his concept was that almost all didymosporous species were generally to be classified in *Arthrobotrys* (exception: *Trichothecium polybrochum*), the phragmosporous species in *Dactylella,* when bearing a single conidium on the tip of the conidiophore, and in *Dactylaria* when more than one conidium is produced in a sympodial manner. That this line could not be drawn sharply was clear to Drechsler (1937), when he classified e. g. *Dactylella asthenopaga* Drechsler in this genus in spite of occasionally branched conidiophore tips. Drechsler (1935, p. 219, and 1937, p. 539) regarded *Monacrosporium* as a synonym of *Dactylella*.

Dactylaria Sacc. is no longer tenable for nematode-trapping species, as the type species, *D. purpurella* (Sacc.) Sacc., has pigmented conidiophores with a denticulate sympodial rhachis; conidia are hyaline or pale brown and septate (Bhatt and Kendrick, 1968). Schenck *et al.* (1977) transferred (almost) all predacious species formerly described in *Dactylaria* to *Arthrobotrys*.

Dactylella was erected by Grove (1884) for hyphomycetes with erect and simple conidiophores bearing a single, multiseptate conidium on the tip. The type species, [p. 4] *D. minuta* Grove, is most probably not capable of capturing nematodes. So far both non-predacious and predacious fungi have been included in *Dactylella*, but if this difference is of taxonomic relevance, then *Dactylella* must be restricted to non-predacious species.

Monacrosporium
Oudemans (1885) introduced *Monacrosporium* for hyaline hyphomycetes, bearing a single, septate conidium at the tip of an erect conidiophore. Oudemans described in this genus two species, *M. elegans* and *M. subtile*, which he had found on rabbit dung, without observing any relationship to nematodes.

Monacrosporium has been used by subsequent authors for several species fulfilling the criteria set up by Oudemans [*M. sarcopodioides* (Harz) Berl. & Vogl. 1886, *M. carestianum* Ferraris 1904, *M. ovatum* Petch 1922*, M. megasporum* Boedijn 1929, *M. tedeschii* Agostini 1933, *M. meliolicola* Cif. 1938, *M. ambrosium* Gadd & Loos, 1947; for references see Chapter 10]. Some of these species have already been transferred to other genera as indicated in the checklist. Clements and Shear (1931) selected *M. elegans* as lectotype. Subramanian (1963) once more designated *M. elegans* as lectotype species, underlining the inflated middle cell of the conidia as the generic criterion, and transferred a large number of (nematode-trapping) *Dactylella* species to *Monacrosporium*.

The *Dactylella-Monacrosporium* complex
Up to the present day the distinction between *Dactylella* and *Monacrosporium* has not been clear.

The revival of *Monacrosporium* by Subramanian was accepted by many, but not all, authors. Drechsler (*e.g.*

1937) regarded *Dactylella* and *Monacrosporium* as synonymous, the former name having priority. Neither could Yadav (1960) and Barron (1968) see a difference between the two genera. Matsushima (1989, 1993) adopted a broad concept of *Dactylella* and included all hyaline species with erect conidiophores, branched or unbranched, and with phragmoconidia, in *Dactylella*, regardless of their conidial shape. Cooke (e.g. 1967 b, 1969) and Cooke and Dickinson (1965), however, described many new species in *Monacrosporium*, and also Castaner (1968) and McCulloch (1977) followed Subramanian. Recently Liu and Zhang (1994) again emphasized the large ventricose cell of *Monacrosporium* conidia whereas, in their opinion, '... the hyalophragmosporic fungi with conidia produced singly and acrogenously on the tips of simple conidiophores ... belong to *Dactylella'*. Furthermore, they left some species with a slightly larger conidial cell (intermediate between *Monacrosporium* and *Dactylella*) in *Dactylella*.

From *Candelabrella* to *Woroninula*
In the last three decades, additional genera were introduced based on minor morphological differences. Subramanian (1963) erected *Drechslerella* for species producing conidia with a thread-like appendage (as *D. acrochaeta* (Drechsler) Subram.). [p. 5]

Rifai and Cooke (1966) found a new species with candelabrum-like conidiophore tips, which they described as *Candelabrella javanica*, and transferred other nematophagous representatives to *Candelabrella*. At the same time Rifai and Cooke (l.c.) regarded a proliferating, geniculate conidiophore tip as being sufficiently different from a conidiophore with short denticles, and classified species with such a geniculate conidiophore in *Genicularia* (nom. illeg., Art. 53 ICBN), which was corrected to *Geniculifera* by Rifai (1975). Cooke (1969) transferred *Trichothecium flagrans* Dudd., a species with a different conidiogenesis, to *Duddingtonia* (honouring C.L. Duddington), while *Trichothecium* is reserved for (non-predacious) species with retrogressive conidiogenesis. The four genera *Drechsleromyces* (type species: *D. atractoides*), *Gangliophragma (*type species: *G. rhopalota*), *Lactydina* (type species: *L. tylopaga*), and *Monacrosporiella* (type species: *M. megalospora*) were proposed by Subramanian in 1977. For their distinction only differences at the level of reproductive structures were taken into account.

Mekhtieva (1979) distinguished as many as nine genera of predacious hyphomycetes, including the new *Dactylariopsis* Mekht. 1967 (type species: *D. brochopaga*), *Golovinia* Mekht. 1967 (type species: *G. bembicodes*), *Nematophagus* Mekht. 1975 (type species: *N. azerbaidzhanicus*), *Kafiaddinia* Mekht. 1978 (type species: *K. fusarispora*), and *Woroninula* Mekht. 1979 (type species: *W. polycephala*), see Chapter 7. The types of trapping organ were neither considered for the generic delimitation nor for the delimitation of sections within a genus.

On the other hand, Schenck *et al.* (1977) broadened the concept of *Arthrobotrys*, because the exclusive criterion of two-celled conidia was found unsatisfactory while the species concerned are closely related. Furthermore they pointed out that 'if a new genus were to be recognized for every Saccardoan conidium type and for every conidiophore type among the nematode-trapping species, a confusing plethora of small genera would result'. For the first time, the predacious activity was taken into account (together with morphology) for the generic classification, when these authors (l.c.) wrote in their emended diagnosis of *Arthrobotrys*: '... trapping nematodes by means of specialized hyphal structures'. However, Schenck *et al.* did not consider all predacious species described until then. When revising *Arthrobotrys*, Van Oorschot (1985) again recognized the additional nematode-trapping genera *Dactylella*, *Duddingtonia*, *Geniculifera*, and *Monacrosporium*, based on conidiophore and conidium morphology.

At present the generic delimitation of the predacious hyphomycetes is far from clear, especially in the *Dactylella-Monacrosporium* complex. The predacious and non-predacious taxa are not delimited at generic level. Many authors (e. g. Dowsett *et al.*, 1984; Barron, 1990) are aware of this confusion and emphasize the need of a reevaluation of the complex.

2.2 Species concepts

Splitting and lumping attitudes have repeatedly conflicted, with a certain predominance for splitting. A scientific basis of the species concept can be expected from careful [p. 6] assessment of variation of a range of isolates grown under the most favourable conditions.

Most species of the *Dactylella-Monacrosporium* complex have been introduced by Drechsler. Herbarium material of species described in the last century often was not available or was found to be in poor condition. Drechsler usually considered his (excellent) drawings as iconotypes and only rarely deposited pure cultures in ATCC and CBS. But, even when dried material in good condition and living (ex-type) cultures were available, some doubts arose and remain about species delimitation. The application of new methods, particularly molecular analyses, are expected to clarify the situation further in the future.

2.3 The present situation

A key to the whole group of nematophagous fungi (including endoparasites) that is still useful was written by Cooke and Godfrey (1964). Its deficiencies are the drawings of sometimes indistinguishable conidia, the now obsolete nomenclature, and the absence of species described in the last 30 years. Cooke (1967 b) prepared a key for the network-forming species of *Monacrosporium*, Castaner (1968) for those species of *Monacrosporium* forming constricting rings. Liu and Zhang (1994) provided a check-list for 38 (plus two new species) and a key for 44 species of *Monacrosporium*, apparently mainly based on literature.

The present study has a wider scope in that as much living material as possible was examined and several non-morphological tests were applied to the isolates in order to estimate the variability of a species.

Not all recognized species were available as living cultures. In some cases original descriptions and drawings had to be reproduced.

3 Material and methods

3.1 Sprinkled-plate technique

The sprinkled-plate technique, as described e.g. by Barron (1977, p. 119), was used to isolate nematophagous fungi: 0.5-1 g of substratum is sprinkled onto a water agar plate. A suspension (1 ml) of the nematode *Turbatrix aceti* Mull. is added as a bait. The presence of predacious fungi is perceived by the appearance of trapped nematodes and the characteristic conidiophores. This method is principally the same as that used by Drechsler, except that he usually used cornmeal agar preinoculated with *Pythium,* and sometimes enriched with other species of nematodes.

3.2 Fungal isolates

The majority of the fungi were isolated from soil samples and plant debris from the Berlin area and from the greenhouses of the Botanic Garden Berlin-Dahlem. Additional soil samples were received or collected from other countries (*e.g.* Thailand and Ecuador). Personal isolates are marked as A.R., the year of isolation and a serial number (*e.g.* [p. 7] A.R. 9310 is the tenth isolate made in 1993). Most of these isolates have been deposited at the Centraalbureau voor Schimmelcultures (CBS). This fungal collection provided about 70 additional strains for studies. Isolates from Lotta Persmark (Lund, Sweden) are marked L.P.

3.3 Agar media and incubation

For the isolation of nematophagous fungi and the induction of trapping organs with added nematodes, water agar (WA) was used: 2% agar (Merck), tap water.

For most other purposes half-strength cornmeal agar (CMA:2) was used: 8.5 g cornmeal agar (Difco), 12.5 g (additional) agar (Merck) and aqua dest. ad 1 l.

Potato-carrot agar (PCA) as an alternative to CMA:2 was prepared as indicated in the CBS Course of Mycology (Gams *et al.,* 1987). Malt-extract agar (MEA, 10 g dry biomalt from Oxoid, 15 g agar (Merck), 10 ml KOH (10 %), aqua dest. ad 1 l, final pH 7) as a rich medium was also tested; however, most isolates formed more aerial mycelium and fewer conidia on this substrate.

Fungi were usually cultivated on agar media in Petri dishes (9 cm diam.). To obtain more biomass for ubiquinone analyses, fungi were grown in liquid cultures on malt-extract solution in 1 litre conical flasks. Colonies were generally incubated at room temperature (approx. 23 ºC) under daylight.

All measurements, unless indicated otherwise, were made from CMA:2 cultures, on which the fungi usually sporulated well. The isolates were then preserved on the same medium as agar slants and stored at 6 ºC with annual transfers. Herbarium specimens were made from CMA:2 cultures, which were killed by a drop of formalin (37 %) and dried at room temperature; they are deposited at CBS.

For the agar media used in several physiological tests the reader is referred to the literature indicated in 6.2.

3.4 Animals and other fungi as prey

The nematode *Turbatrix aceti* was used as a bait for the soil sprinkling technique and for the induction of trapping organs in pure cultures. This bacteria-feeding species was cultivated on an non-sterile oat-porridge, which served as food for bacteria. The nematodes were transferred every four to six weeks to a fresh medium. Before seeding a sprinkled plate, nematodes were cleaned from this substratum by passage through a Baerman funnel. Additional experiments were carried out with *Amoeba proteus*, *Enchytraeus crypticus* and the collembolan *Onchiurus fimatus*.

Several Oomycete species (*Pythium intermedium, P. oligandrum, P. silvaticum,* and *P. ultimum*) were added to cultures of *Dactylella spermatophaga*.

3.5 Microscopic mounts

All measurements were made in (tap) water mounts. Conidia were measured at a magnification of 1250 x (with an estimated accuracy of ± 0.4 µm). When three figures [p. 8] are given, the central one represents the arithmetic means, and is based on approx. 25 measurements.
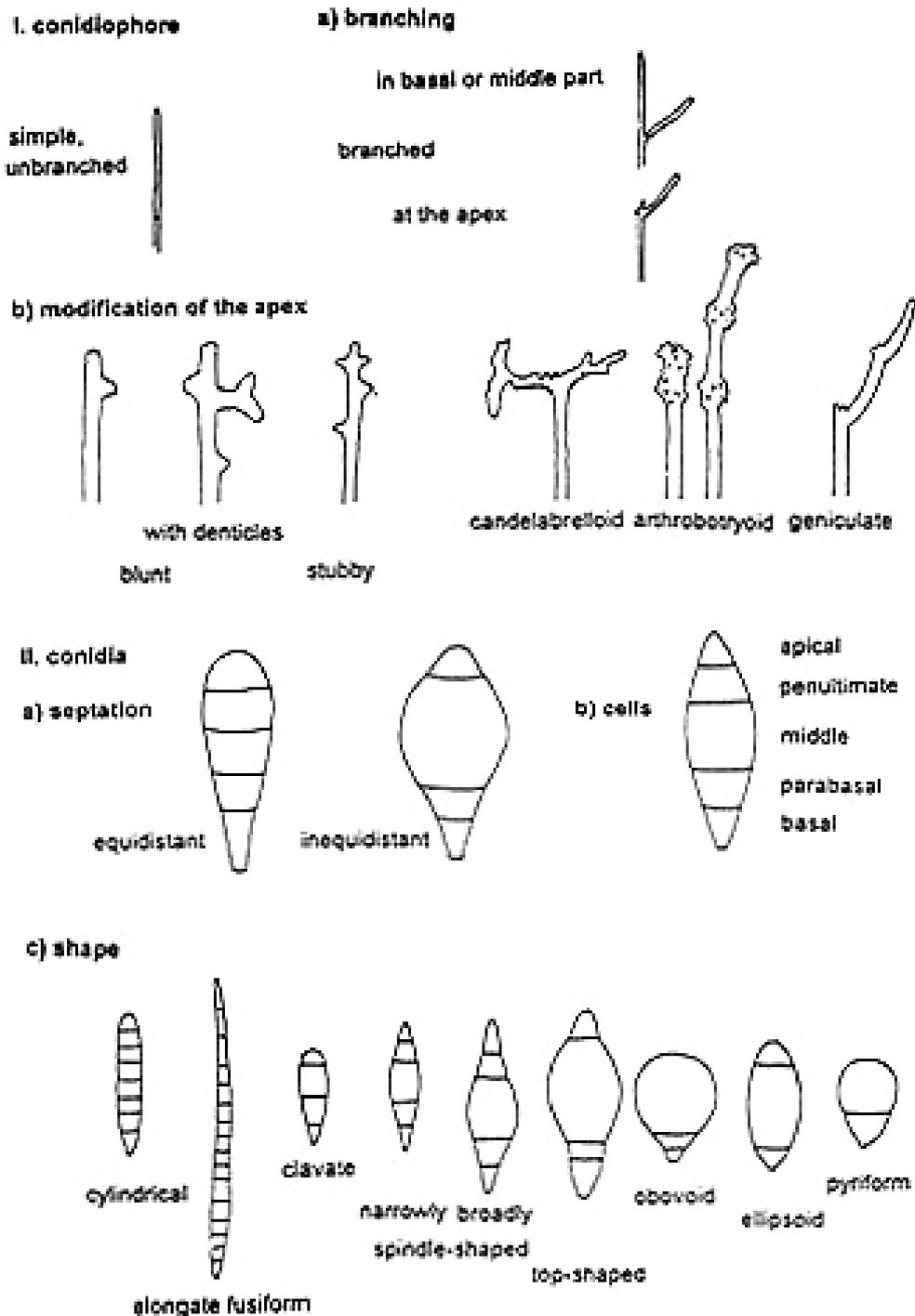
I. conidiophore

a) branching

in basal or middle part

simple, unbranched

branched

at the apex

b) modification of the apex

blunt

with denticles

stubby

candelabrelloid arthrobotryoid geniculate

II. conidia

a) septation

equidistant

inequidistant

b) cells

apical

penultimate

middle

parabasal

basal

c) shape

cylindrical

clavate

elongate fusiform

narrowly broadly

spindle-shaped

top-shaped

obovoid

ellipsoid

pyriform

Fig. 1. Conidiophore types, conidial septation, cells, and shapes - mostly after Drechsler (1937, 1943, 1950) in the *Arthrobotrys-Dactylella-Monacrosporium* complex. Species of which conidia are illustrated in II c, from left to right: *D. rhopalota, M. leptosporum, M. asthenopagum, M. haptotylum, M. ellipsosporum, M. elegans, M. eudermatum, M. heterosporum, A. oligospora.*

3.6 Ubiquinone analysis

The method of Kuraishi *et al.* (1985) was followed, using a 1040 M diode-array detector from Hewlett Packard at 270 nm, with a column from Merck 50943 LiChro CART R. The isocratic solvent system isopropanol-methanol 35 : 65 was used; the flow rate was 1 ml/min at 30 ºC. The injection volume depended on the sample: between 50 and 200 μl. The reference substances were Q-10 from heart of cattle (Merck), Q-10(H2) from *Aspergillus flavus*, and Q-9 from *Galactomyces geotrichum*.

3.7 Growth rate and temperature test

Plates were incubated at 5, 10, 15, 20, 25 and 30 ºC in constant-temperature chambers (Heraeus). The colony radius was recorded on the fifth day (after the fungus had started to grow well) and on the eighth day. The difference between these two radii was recorded.

3.8 Physiological-biochemical tests

The cellulose degradation potential was determined by a modified cellulase test after Hazra *et al.* (1958, as described in Kreisel and Schauer, 1987): fungi were incubated on water agar enriched with 10 g/l cellulose powder. After four to ten days (depending on the growth rates of the isolates), the Petri dishes were flooded with chlor-zinc-iodine. In the positive case, the agar remains uncoloured (more or less yellow) below the colony, while plates with a negative result turned purple to brown. Absence of purple staining in the colony centre was taken to indicate cellulolytic activity.

A modified polyphenol oxidase test after Tichy *et al.* (1962, described in Kreisel and Schauer, 1987) was tried. Instead of MEA the fungi were grown on CMA:2. Guayacol vapour was supplied as substrate by pouring 10 ml into the lid of a reversed Petri dish. After several hours of incubation (4-72 h) a positive reaction was indicated by a red to purple colour of the colony.

3.9 Fluorescent staining of nuclei

To observe the nuclei in conidial and in hyphal cells, they were stained with DAPI (= 4',6-diamidino-2-phenylindole) (dye solution: 0.1 μg DAPI (SERVA) in 1 ml distilled water). [p. 9]

4 Morphological studies

Species of the *Dactylella-Monacrosporium* complex are characterized by a rather fast-growing hyaline septate mycelium, erect conidiophores bearing conidia on the tip, and hyaline conidia that are at least one-septate. In addition, many of the species are able to form trapping organs of some kind enabling them to capture microscopical animals, such as nematodes, rhizopods, copepods or collembola. A small group can parasitize Oomycetes of the genus *Pythium* by developing appressoria or haustoria on and inside the oogonia and zoosporangia of the host. A third group is non-predacious and non-parasitic and has not been seen to produce any special structures to exploit other organisms.

In this and the following chapters, *Arthrobotrys* has also been included as it is closely related.

4.1 Conidiophores (Fig. 1, I)

Conidiophore length usually falls within the range 200-400 μm. The total range, however, is between 10 μm (*D. helminthodes*) and 500 μm (*e.g. M. doedycoides*). Conidiophore width at the base is 2.5-7.5 μm, at the top 1.5-3.5 μm. In many species the conidiophores are acropetally modified by proliferations which can be described as geniculate, candelabrelloid or arthrobotryoid. Very often, especially in *Monacrosporium*, the conidiophores produce short branches or ramifications near the tip, which have been called spurs, denticles (*e.g.* Cole and Samson, 1979), pegs (Barron, 1968) or sterigmata (Drechsler, *e.g.* 1937). These short branches (Fig. 1, I b) can be perpendicular from a dominant vertical axis or at oblique angles, giving rise to branches of approximately equal width. If these branches are very short ('stubby'; Drechsler, 1937), as in *M. haptotylum*, then a bunch of conidia is observed resembling the clusters of *Arthrobotrys* species.

Modifications of conidiophore tips have partly led to the distinction of genera. In any case, they are regarded as a rather stable feature, even if the occasional appearance of an additional denticle or a geniculate branch can be observed in a species known as generally having simple conidiophore tips (*e.g. M. leptosporum*). A pronounced and regularly occurring number of denticles (*e.g. M. thaumasium, M. haptotylum*), a pronounced geniculate (*e.g. A. perpasta*) or arthrobotryoid conidiophore tip (*e.g. A. oligospora*) can still be regarded as specific.

The term 'conidiophore branching', however, primarily describes long branches that may arise along the whole length of the conidiophore, except for the tip. Such branching is not regarded as having high taxonomic value as it
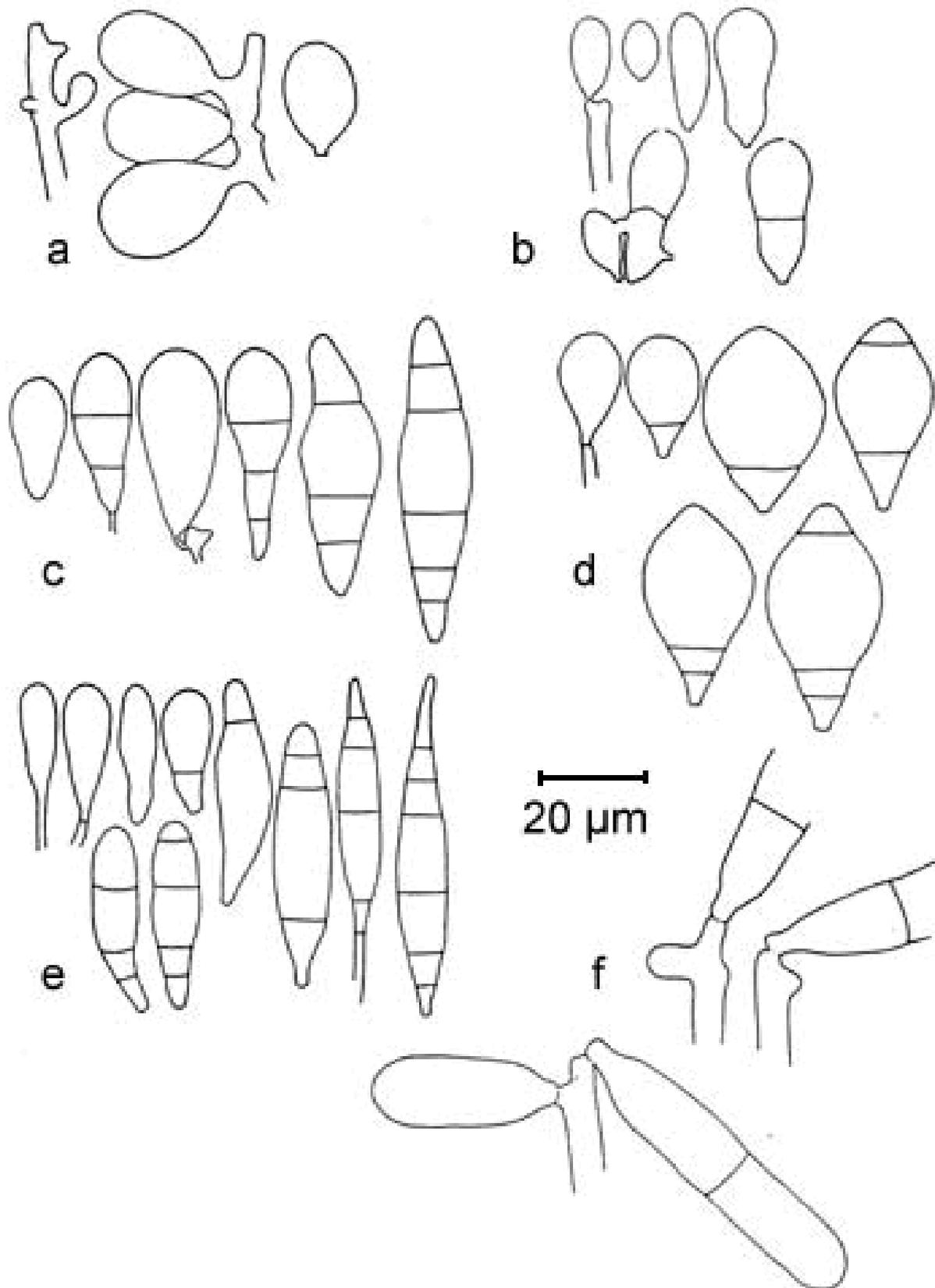
Fig. 2. Examples of conidial development and shapes in
Arthrobotrys, Dactylella, Monacrosporium and *Duddingtonia*.
a. *A. amerospora,* b. *A. conoides,* c. *M. gampsosporum,*
d. *M. thaumasium,* e. *D. oxyspora,* f. *Duddingtonia flagrans.*
Light-microscopic observations. [p. 13]

may occur, or be absent, in one and the same species (*e.g. M. doedycoides*). [p. 10]

Fig. 1.
Conidiophore types, conidial septation, cells, and shapes - mostly after Drechsler (1937, 1943, 1950) in the *Arthrobotrys-Dactylella-Monacrosporium* complex.
Species of which conidia are illustrated in II c, from left to right:
D. rhopalota, M. leptosporum, M. asthenopagum, M. haptotylum, M. ellipsosporum, M. elegans, M. eudermatum, M. heterosporum, A. oligospora.[p. 11]

4.2 Conidiogenesis (Fig. 2)

Three phases can be distinguished in the development of blastoconidia in this group: (1) The conidia are blown out *de novo*, the tip of the conidiophore enlarges before a septum is formed (Fig. 2, a, e); all wall layers of the conidiogenous cell contribute to the conidial cell wall (= holoblastic). (2) Conidial secession is schizolytic (in some species of *Arthrobotrys* conidia may remain firmly attached to the conidiogenous cell and are liberated with difficulty rhexolytically, retaining cell wall fragments of the conidiogenous cell on the conidial base). (3) The conidiogenous cell may produce only one conidium, but in many cases more than one conidium is formed by the conidiogenous cell by sympodial proliferation, the branches not being separated by a septum from the main axis. Since the conidia are not produced at the same time; this proliferation is called sympodial. In contrast to most species of *Arthrobotrys*, the conidiiferous apex of species of the *Dactylella-Monacrosporium* complex never swells.

Hawksworth *et al.* (1983) categorize *Dactylella* as producing hyaline, multiseptate conidia (*Hyalophragmiae*) on simple conidiophores with a holoblastic conidiogenesis and a sympodial conidiophore growth. *Monacrosporium*, however, is classified by them among the *Phaeophragmiae*, indicating pigmented conidia, and as producing synnemata (probably unintentional errors). De Hoog and Van Oorschot (1985) distinguished *Dactylella* and *Monacrosporium* from most of the other genera of the *Dactylaria* complex by thallic conidiogenesis. This interpretation is erroneous, because the conidia are blown out from a set conidiophore tip, contrasting with solitary thalloconidia of *Trichophyton* and *Microsporum*.

The conidiogenesis basically seems to be the same for all representatives of the complex. One exception is *Duddingtonia flagrans* (Dudd.) R.C. Cooke, which forms a series of broadly attached conidia at the apex, usually without discrete denticles (Fig.1, II f).

4.3 Conidia (Fig. 1, II)

Conidia vary in shape, septation, and size. The conidial shape is described as spindle-shaped (= fusiform), clavate, cylindrical, ellipsoidal, pyriform, obovoid, top-shaped (= turbinate) (Fig. 2, II c). Septation of conidia occurs in all species; one septum is found in *Arthrobotrys*-type conidia of some species formerly classified in *Geniculifera*. The *Pythium*-parasitizing *Dactylella stenomeces* can produce as many as 21 septa per conidium. The septa within a conidium are either equidistant or inequidistant (Fig. 2, II a). The shortest conidia are those of *M. asthenopagum* with 20 μm (minimum length), the narrowest ones those of *A. haptospora* with 2.2-3.2 μm width. The length : width ratio varies between 1.5 (subglobose) and 21 (very slender).

Microconidia can be formed in some species in addition to macroconidia. They are of smaller size, are formed on shorter conidiophores, and usually appear later. (As an exception *Monacrosporium gephyropagum* CBS 178.37 now only produces microconidia.) [p. 12]
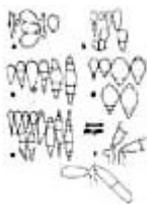

Fig. 2.
Examples of conidial development and shapes in *Arthrobotrys, Dactylella, Monacrosporium* and *Duddingtonia*.
a. *A. amerospora; A. conoides;* c. *M. gampsosporum;* d. *M. thaumasium;* e. *D. oxyspora* ;
f. *Duddingtonia flagrans.* Light-microscopic observations. [p. 13]

Microconidia usually are infrequent. Barron (1979) summarized the knowledge of microconidial sporulation for predacious fungi, registering microconidia in three *Arthrobotrys* species with constricting rings.

The morphology of the conidia and the conidiophores provides a number of features on which taxonomy can be based. Because of their unreliable presence or absence, microconidia are of limited taxonomic value.

Both macroconidia and microconidia may germinate with their characteristic trapping organ as it has been shown for some species with constricting rings (Barron, l.c.).

4.4 Chlamydospores

Resting spores with more or less thickened walls are found in many species of the *Arthrobotrys-Dactylella-Monacrosporium* complex. They develop especially in older cultures, in the agar or in the trapped nematode. They are formed terminally or intercalarily, singly or in chains, and are smooth-walled or warted. The chlamydospores of *A. oligospora* are only produced in media devoid of carbon sources (Scholler and Rubner, 1994). Chlamydospores are probably the only structures of these fungi that are somewhat resistant to heat, toxic chemicals, and drought.

Cooke and Satchuthananthavale (1965) suggested that the production of 'chlamydospores cannot be used reliably to distinguish between species in the nematode-trapping series' when discussing the differences between *Dactylaria haptotyla* Drechsler and *D. sclerohypha* Drechsler. The latter species is known to form 'resting bodies' (= chlamydospores) externally or by thickening of the assimilative hyphae in the nematode. The conidia and the conidiophore resemble *D. haptotyla*, so that the only 'significant' difference between these two species would lie in the production of these resting bodies.

In the course of this revision, chlamydospores were found in species where they had not been described previously, *viz. M. ellipsosporum* (A.R. 9143), *M. eudermatum* (CBS 584.91, A.R. 9132, A.R. 925, A.R. 9315)*, M. reticulatum* (CBS 201.50), *M. psychrophilum* (CBS 319.94, L.P. 901), *D. oxyspora* (CBS 157.89), and *D. atractoides* (CBS 310.84).

In some of the cultures, chlamydospores could be observed after a long time (up to 2 months) or after incubation at other temperatures than room temperature. Thus, chlamydospores are quite common among *Arthrobotrys* and *Monacrosporium* species, though they do not appear regularly and under all circumstances. Furthermore, some of the species described without chlamydospores were found to produce them, without justifying the distinction of a new taxon. But the morphology (single or in chains, smooth or warted, thin- or thick-walled) remains significant.

4.5 Organs of capture (Figs 3, 4, 5, 6, 7 and 8)

The morphology and functioning of trapping organs have been the subject of many publications. Barron (1977) summarized the different types, which are listed and explained below. Four types (4.5.1-4.5.3 and 4.5.5) have in common a mucous substance [p. 14] that wholly or partly covers the trapping devices and is sticky for nematodes. The chemical composition of the adhesive layer of networks (*e.g.* of *A. oligospora*) has been analysed. Lectines were found with an affinity to the carbohydrates of the nematode cuticle (Nordbring-Hertz, 1988). Extracellular polymers (sugars, uronic acids and proteins) mediate the adhesion and represent the site for enzymes, which are important for the infection and penetration of the host (Tunlid *et al.*, 1991). It is probable, though not yet proven, that the mucous substance which covers trapping devices other than networks consists basically of the same compounds. The course of events after trapping the nematodes - penetration of the cuticle, formation of an infection bulb from which the assimilative hyphae grow into the prey - is the same for all other types of trapping organs. Friman (1993a) has summarized the knowledge of the infection process, listing investigators and species so far investigated.

4.5.1 *Unstalked knobs* (Fig. 3)
The knobs are more or less globose cells, obovoid or prolate-ellipsoid, single or proliferating. Measurements are given for:
- *M. lobatum*: 9-13 x 8-9 µm (Duddington, 1951),
- *M. phymatopagum*: mostly 6-9.5 x 3.8-5.5 µm (in greatest width) (Drechsler, 1954),
- *M. parvicolle*: 6.5-11 x 5.5-9 µm (Drechsler, 1962), and
- *M. robustum*: 16-24 x 9-10 µm (McCulloch, 1977).

The tendency to proliferate is high in most of these species: *M. lobatum* as well as *M. parvicolle* can produce chains of knob-like cells (up to 12) which bend and sometimes close to form a ring. *M. arcuatum* can produce arches, rings and networks by branching and anastomosis (Scheuer and Webster, 1990).

The knobs are entirely covered by an adhesive substance. Sometimes the struggling nematode, which tries to escape, tears off the knob and carries it away. The knob, however, has not lost its infectious potential and later germinates and penetrates the nematode.

4.5.2 *Hyphal branches* (Fig. 4)
The short, adhesive branches consist of one to several elongated cells. These trapping organs occur densely side-by-side and tend to anastomose. Then arches or bridges are formed, but they remain two-dimensional, in contrast to the three-dimensional networks (4.5.5). The ability of the hyphal branches to form bridges (scalariform) was used as a main criterion to separate *M.cionopagum* (simple branches) from *M. gephyropagum* with anastomosed branches (Drechsler, 1950; Cooke and Godfrey, 1964). However, the change from one kind to the other is fluent. The difference between branches and knobs may not be very sharp, at least not for *M. robustum*, which forms elongated protuberances rather than spherical knobs. Whether these elongated protuberances proliferate under certain circumstances, was not mentioned by McCulloch (1977). If they do proliferate, this trapping organ should be grouped within the hyphal branches. [p. 15]
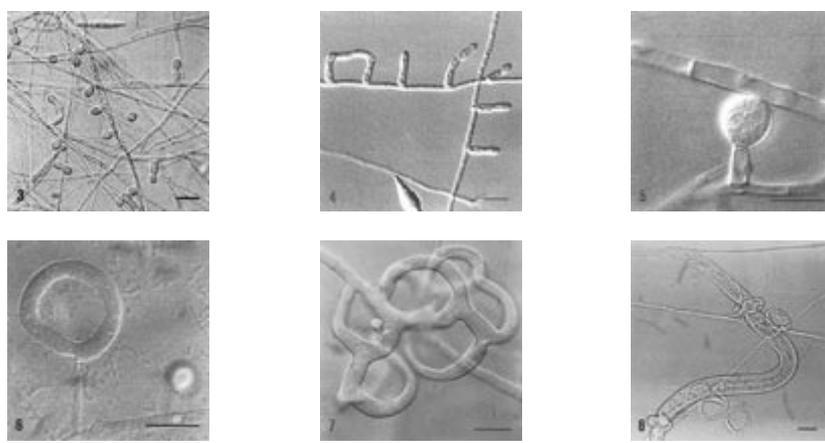
Figs 3-8
Types of trapping organs in species of *Arthrobotrys* and *Monacrosporium.-*
3. unstalked knobs, single or proliferating
(*M. arcuatum*, CBS 174.89)
4. hyphal branches (*M. gephyropagum*, A.R. 9225)
5. stalked knob (*M. mammillatum*, CBS 486.63)
6. non-constricting ring and stalked knob (out of focus) (*M. haptotyplum*, A.R. 9324)
7. three-dimensional network (*A. conoides*, A.R. 9334)
8. constricting rings with nematode (*M. doedycoides*, A.R. 901). Scale bars = 20 µm (3, 4, 7, 8), 10 µm (5, 6). [p. 16]
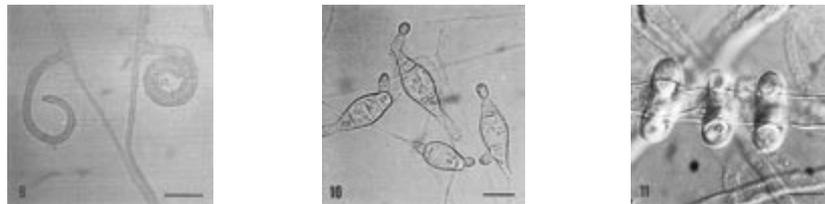
Figs 9-11
9. Degenerated constricting rings (*M. doedycoides*, CBS 175.55)
10. conidia with adhesive branches (*M. gephyropagum*, L.P. 9025)
11. *A. oligospora* (A.R. 9113), coiling around *Rhizoctonia solani*.
Scale bars = 20 µm (9, 10), 10 µm (11).

The close relationship between knobs and hyphal branches is illustrated in *M. arcuatum* (CBS 174.89, Fig. 18) by the spherical adhesive outgrowths of ripe (germinating?) conidia and the elongated outgrowths from hyphae.

4.5.3 *Stalked knobs* (Fig. 5)
The length and width of the stalk can vary considerably. *M. parvicolle*, listed as having unstalked knobs, may also form stalks (0.5-3.5 x 2-3.5 µm; Drechsler, 1962). The stalks of *M. ellipsosporum* are intermediate between the stout stalks of *M. parvicolle* and the long stalks of several other species: 5-10 µm long with much variation, and 2.4-3 µm wide, mostly unicellular (Drechsler, 1937). Even longer stalks can measure between 4 and 15 µm in length and 1-1.4 µm in width, as observed in *M. haptotylum* (as *Dactylaria candida*; Drechsler, 1937). Only the apical globose cell is covered with adhesive material, not the stalk. Long-stalked knobs may be accompanied by non-constricting rings in some species. [p. 17]

4.5.4 *Non-constricting rings* (Fig. 6)
Three ring cells are supported by a slender stalk. Drechsler (1937) measured 15-23 µm in outer diameter for *M. haptotylum (*as *D. candida*), 13-22 µm for *M. leptosporum*. Shome and Shome (1966) reported 14.7-17 µm for *Dactylaria dasguptae* (= *M. leptosporum*). The stalks are described as being longer (more slender) than the ones of constricting rings: 10-35 µm long in *M. haptotylum* (*D. candida*), 8-8.5 µm in *D. dasguptae*.
Non-constricting rings are not seen frequently, due to the small number of species producing them and the unreliability of their production in a species known to do so. Non-constricting rings are easily detached from the mycelium and carried away by a (trapped) nematode.

4.5.5 *Networks* (Fig. 7)
Most of the *Arthrobotrys* species and about one third of the species of the *Dactylella-Monacrosporium* complex develop loops connected to form three-dimensional networks. This type of reticulate trapping organ has been investigated in many aspects by Nordbring-Hertz (1972, 1977), and with co-workers (1978, 1989).
An exception to the three-dimensionality of the networks is only known for *Arthrobotrys musiformis*, where the networks are less luxuriant and often described as two-dimensional; but they differ from the two-dimensional scalariform structures described above (4.5.2) by rounder arches and the occasional three-dimensional structure.

4.5.6 *Constricting rings* (Fig. 8)

Constricting rings are morphologically similar to non-constricting rings except for the trapping mechanism, the length and width of the stalks, and a slight internal widening of the ring cells. Their fairly frequent occurrence may be due to the ecological advantage offered by their trapping efficiency. The mechanism of constriction has been the object of several studies (Couch, 1937; Muller, 1958; Heintz and Pramer, 1972; Dowsett and Reid, 1977 a; Barron, 1979; Zachariah, 1989). The closure within 0.1 sec. is the fastest non-disruptive movement known within the plant and fungal kingdoms.

The rings are typically arranged in rather dense rows on the parental hyphae, with the stalks standing up vertically and the rings in a right angle to the hyphae. The ontogeny has been described repeatedly (*e.g.* Barron, 1977). The ring diameter can vary considerably within one strain, and more so between different strains and species. Drechsler (1954) indicated 20-42 µm outer diameter for *A. anchonia*; rings with diameters up to 130 µm are sometimes produced on Difco CMA by *A. brochopaga*, the trap cells measuring 110 x 10 µm, besides normal rings with cells 20 x 5 µm (Turnbull and Zachariah, 1978; G. L. Barron, pers. comm.).

4.6 Taxonomic value of the trapping organs

Predacious species of the complex have in common their ability to produce organs of capture and to trap and digest nematodes (rarely also rhizopods, copepods, or springtails) which provides ecological advantages over non-predacious species. The highly [p. 18] differentiated trapping organs are quite constant in a species and seem to have a high taxonomic value (see Discussion, 6.3).

Experience has shown that the development of trapping organs is a constant feature, at least when certain conditions for their development are suitable (i.e. animal- or substrate induction). The trapping organs also remain stable over the years of culturing. In the fresh material studied (180 isolates), no fungus of *Arthrobotrys* and *Monacrosporium* was found that did not develop them. But even old strains, which most probably had suffered some degeneration, had seldom lost the ability to produce trapping organs.

Degeneration of cultures of predacious fungi can be a great problem in culture collections. Until recently it was almost impossible to preserve them in a lyophilized state so as to preserve all morphological and biological features. Species with large, thick-walled conidia do not withstand fast cooling (Tan *et al.*, 1994) but, with a modified treatment, good preservation can now also be assured.

Forty-eight strains of the *Arthrobotrys-Dactylella-Monacrosporium* complex preserved in CBS are known from the literature to form trapping organs (Table 1). Two additional strains listed, which had not been known to form trapping organs, were found to do so; CBS 229.52 had been wrongly identified as *Dactylella heptameres*, and in the other, *Laridospora appendiculata*, CBS 226.64, a new character was observed. Table 1 lists these 50 strains and the type of trapping organ produced. Thirty-six of these strains could still form their characteristic trapping organs. Of twelve strains which did not develop trapping organs seven did not sporulate either. Their identity cannot be verified by morphological means. The remaining five strains sporulated, but could only partly be identified as nematophagous species. The identity is still doubtful in '*Dactylella asthenopaga*' CBS 262.83 and 917.85, originally described as having stalked knobs. Especially CBS 917.85 with its salmon-pink colony colour and abundant sporulation has conidiophores deviating from *D. asthenopaga* (*M. asthenopagum* (Drechsler) A. Rubner), but it was not possible to consider the strain as a separate species.

Dactylella polybrocha CBS 319.56, *Geniculifera effusa* CBS 774.84, and *M. doedycoides* CBS 175.55 (Fig. 9) form rings which are degenerated and unable to capture *Turbatrix aceti*. This suggests that constricting rings are the type of trapping organ most sensitive to degeneration in culture.

At the species level the type of trapping organ is considered to have high taxonomic significance. As a rule, a species can only form one type of trapping organ. Three modifications of this rule are noted:
a)   Non-constricting rings may be accompanied by stalked knobs.
b)   Within the knob-forming fungi a variation in the length of the stalk can be observed. The proliferation of knobs, as seen in *M. parvicolle*, sometimes resembles the hyphal branches of *M. gephyropagum*.
c)   The simple hyphal branches ('*M. cionopagum*') tend to fuse, forming a two-dimensional network (*M. gephyropagum*). [p. 19]

Table 1: Trapping organ formation in 50 strains of hyphomycetes from the CBS known to capture nematodes or revealing their nematophagous capacity during this study (strains in parentheses). The type of trapping organ (from the literature), the actual capability of forming the trapping organs after induction with *Turbatrix aceti*, and the presence of conidia are indicated. *A.* = *Arthrobotrys*, *D.* = *Dactylella*, *G.* = *Geniculifera*, *L.* = *Laridospora*, *M.* = *Monacrosporium*.

Species (name as received)	strain	trapping organ (as described)	prod. in culture	conidia	reidentified as
A. javanica	534.63	adhesive network	+	+	
A. pyriformis	221.54	adhesive network	+	+	
A. vermicola	513.66	adhesive network	+	+	
A. scaphoides	226.52	adhesive network	+	+	
D. arcuata	174.89	adhesive hyphal branches	+	+	
L. appendiculata	206.64	---	(st. knobs)	-	*M. tentaculatum*

Species		Trapping organ			
D. asthenopaga	227.52	stalked knobs	-	-	
	222.54	stalked knobs	-	-	
	262.83	stalked knobs	-	+	
	917.85	stalked knobs	-	+	
M. bembicodes	177.37	constricting rings	-	-	
	160.38	constricting rings	+	+	
	132.42	constricting rings	(network)	+	*M. thaumasium*
	846.70	constricting rings	(branches)	-	*M. gephyropagum*
	703.74	constricting rings	(network)	-	
G. bogoriensis	437.82	adhesive network	+	+	*M. thaumasium*
D. candida	200.50	stalked knobs	+	+	
	220.54	stalked knobs	+	+	
M. cionopagum	228.52	hyphal branches	+	-	
G. clavispora	545.63	adhesive network	+	+	
G. cystosporia	130.83	adhesive network	+	-	
M. doedycoides	233.54	constricting rings	+	-	
	175.55	constricting rings	-	+	
M. drechsleri	549.63	stalked knobs	+	+	
G. effusa	774.84	constricting rings	-	+	
M. ellipsosporum	224.54	stalked knobs	+	-	
	225.54	stalked knobs	+	+	
G. eudermata	770.85	adhesive network	+	+	*M. thaumasium*
D. gampsospora	512.61	adhesive network	+	+	
M. gephyropagum	178.37	hyphal branches	+	+	
	197.73	hyphal branches	+	+	[p. 20]
D. haptotyla	546.63	stalked knobs	-	-	
	757.85	stalked knobs	+	+	
D. heptameres	229.52	---	(branches)	+	*M. gephyropagum*
D. lobata	227.54	proliferating knobs	-	-	
	228.54	proliferating knobs	-	-	
D. lysipaga	486.63	stalked knobs	+	+	*M. mammillatum*
M. mammillatum	229.54	stalked knobs	+	-	
D. multiformis	773.84	adhesive network	+	+	
M. parvicolle	219.61	proliferating knobs	+	+	
M. phymatopagum	325.72	unstalked knobs	+	-	
D. polybrocha	319.56	constricting rings	-	+	
G. psychrophila	547.63	adhesive network	-	-	
	548.63	adhesive network	+	+	
	548.63	adhesive network	+	+	
	436.82	adhesive network	+	+	*M. thaumasium*
M. reticulatum	201.50	adhesive network	+	+	
	550.63	adhesive network	+	-	
M. rutgeriense	769.85	adhesive network	+	+	*M. eudermatum*
M. thaumasium	128.83	adhesive network	+	+	
	176.37	adhesive network	+	+	

4.7 Trapping organs developed from conidia (Fig. 10)

Conidia (diaspores) of many species also carry an infection potential, particularly in the knob-forming species. In *M. parvicolle* and *M. arcuatum* adhesive cells are regularly formed on the apical and/or basal cell of mature conidia. Some types of trapping organs develop spontaneously, some require induction by nematodes. The same is observed for the conidia. If a strain can develop knobs or constricting rings without induction on the mycelium, its conidia will do likewise. The conidia of network-formers, particularly *A. oligospora*, need to come in contact with certain diffusing substances of cow dung in order to germinate with three-dimensional loops (Dackman &

The ecological advantage of this phenomenon, which is comparable to the strategies of endoparasites (infection only by conidia), can be explained as follows:

1. Under conditions of nutrient shortage, an early-trapped prey provides nourishment for the young developing fungus.

2. The infected motile nematode contributes to the dispersal of the species, remaining alive for a certain time and carrying the fungus away (zoochory). [p. 21]

4.8 Hyphal coils and mycoparasitic action

Hyphae of nematode-trapping species may coil around the hyphae of a susceptible fungus, such as *Rhizoctonia solani*. These coils (Fig.11) have about twice the diameter of the normal hyphae and can easily be observed by light microscopy (Tzean & Estey, 1978). Persson (1991) showed that the cytoplasm of the host cells eventually disintegrates, though it is not penetrated by the parasite. Therefore the hyphal coiling is interpreted in terms of competition for nutrients and not as a means of gaining nutrients directly from the host.

Arthrobotrys oligospora is the best studied species, but also *A. superba*, *A. entomopaga* and *M. haptotylum* are known to form hyphal coils around *Rhizoctonia solani* (Persson *et al.*, 1985).

5 Taxonomic outlook

Species of the *Dactylella-Monacrosporium* complex belong to a rather uniform group of imperfect fungi without dark pigments deposited in their mycelium, conidiophores or conidia (Moniliaceae, Phragmosporae). Only the resting bodies (chlamydospores) are sometimes pigmented with yellow or light brown substances. In addition, the mass of conidia of a well-sporulating culture can give a tinge of pink or yellow (especially strains of *Arthrobotrys*). Pink or salmon pigments are often produced when cultures are exposed to UV-light, suggesting a protection against harmful radiation.

5.1 Teleomorph connections

While *Nematoctonus* Drechsler is known as the anamorph of *Hohenbuehelia* Schulzer (Basidiomycota, Agaricales), the ascomycete affinity of the *Dactylella-Monacrosporium* complex has never been questioned. Hyphal septa in *Dactylella lysipaga* show a simple pore with two associated Woronin bodies (Wimble and Young, 1983).

A relationship with certain discomycetes has been suggested by several authors. Drechsler (1937, p. 458 and fig. 18) depicted the appearance of apothecia in a culture of *Arthrobotrys superba*. They were flesh-coloured, 0.5-0.8 mm in diameter, somewhat stalked and with a prominent marginal border. The cylindrical asci measured 29-32 µm in length and about 3 µm in width. Ascospores were hyaline and tear-shaped (5 x 1.3 µm). Drechsler did not succeed in proving the conspecifity of *Arthrobotrys* and this discomycete since it had developed in a wormy agar plate culture, and contamination could not be ruled out. It seems very probable that Drechsler's discovery was not an infection, if it is compared to the apothecia of *Orbilia fimicola* Jeng & Krug found to be associated with this species (Pfister, 1994).

Pfister (l.c.) isolated ascospores of *Orbilia fimicola* and obtained *Arthrobotrys superba* as its anamorph. Another anamorph, associated with *Orbilia xanthostigma* (Fr. : Fr.) Fr., is *Dicranidion fragile* Harkn. Matsushima (1995) established the connection of *Orbilia trinacriifera* Mats. with a *Trinacrium* anamorph. For both fungi no nematophagous activity is specifically known (but see under 5.2). [p. 22]

Zachariah (1983 a) induced apothecia when crossing an auxotrophic strain of *Arthrobotrys dactyloides* with a prototrophic strain. The ascocarps developed on a stroma, and measured about 225 µm in diameter. However, no asci were formed. A teleomorph connection of the non-nematophagous *Dactylella rhopalota* Drechsler was discovered by Thakur and Zachariah (1989): after treatment with bacteria, *D. rhopalota* developed ascocarps resembling *Orbilia*. According to Baral (pers. comm.), this is probably *O. inflatula* (P. Karsten) P. Karsten, however, this species is better placed in another genus.

The coenzyme Q-10(H2) system found to be present in four species of the *Arthrobotrys-Dactylella-Monacrosporium* complex (see 6.2.6) is additional evidence of their ascomycete relationship.

5.2 Nematode-trapping fungi of other taxonomical groups

For the sake of completeness the anamorph-genera *Tridentaria* Preuss, *Triposporina* Höhnel and *Pedilospora* Höhnel (= *Dicranidion* Harkn., fide Peek and Solheim (1958)) are to be mentioned here. They trap nematodes without special structures and their conidial apparatus has no similarity with the group of hyphomycetes considered in this revision. *P. dactylopaga* Drechsler (1934), however, captures amoebae with adhesive protuberances. Hyphae

of *Tridentaria implicans* Drechsler encircle the captured nematodes, then resembling non-constricting rings (Drechsler, 1940). *Haptocara latirostrum* Drechsler produces adhesive hyphal protuberances and subglobose adhesive cells arising from the conidia (Drechsler, 1975).

Besides anamorphic Ascomycota, obligately or facultatively predacious fungi have been described so far from the Zygomycota (*Zoopagales*), and the Basidiomycota (*Tricholomataceae, Pleurotaceae* and *Corticiaceae*). The amoebae- and nematode-capturing genera of *Zoopagaceae* (*Zoopage* Drechsler, *Acaulopage* Drechsler, *Cystopage* Drechsler, *Stylopage* Drechsler) do not develop any special organs of capture but exude adhesive cushions from undifferentiated hyphae. [Also the rotifer-capturing genus *Zoophagus* Sommerst., with specialized adhesive pegs, has been shown to belong to the *Zoopagales* (Dick, 1990; Morikawa *et al.*, 1993)].

Basidiomycetes of the anamorph-genus *Nematoctonus* Drechsler (teleomorph *Hohenbuehelia* Schulzer) form hourglass-shaped knobs covered with an adhesive substance (Thorn and Barron, 1986). *Pleurotus ostreatus* (Jacq. : Fr.) P. Kumm. and other species of this genus secrete small droplets of toxin from spathulate cells and thus immobilize nematodes (Barron and Thorn, 1987). Recently another basidiomycetous genus, *Hyphoderma* Wallr., was found to capture or to poison and then consume nematodes. The predacious species of *Hyphoderma* capture their prey by means of stephanocysts, one- or two-celled structures covered with mucilage (Tzean and Liou, 1993). [p. 23]

5.3 Hyphomycetes predacious on microscopic animals other than nematodes

Tridentaria species, such as *T. implicans* Drechsler, do not only capture nematodes, but also rhizopods.

Arthrobotrys entomopaga Drechsler and *A. ferox* Onofri & Tosi are known to capture springtails. Their trapping organs resemble the previously described stalked knobs (4.5.3) with a copious adhesive covering the globose knob ('vesicle', Onofri and Tosi, 1992). These organs obviously mimic spermatophores of the animals which, therefore, get easily trapped (W. Gams, pers. comm.). Drechsler (1944 b) reported *A. entomopaga* as occasionally destroying various nematodes.

One *Monacrosporium* species, *M. copepodii* (G.L. Barron) A. Rubner, has been found to prey on copepods. It develops hyphae or lateral branches with a swollen, sometimes globose end. Adult and larval stages of copepods adhere to the adhesive substance and are penetrated by the fungus (Barron, 1990).

Tzean and Barron (1983) described *Cephaliophora navicularis*, the first fungal species known to capture bdelloid rotifers. Peg-like outgrowths with an adhesive layer are formed on the hyphae as well as on the conidia. Subsequently *C. muscicola* and *C. longispora* were discovered to capture rotifers and tardigrades (Barron *et al.*, 1990). Morikawa *et al.* (1993) investigated *Cephaliophora, Zoophagus*, and *Lecophagus* by light- and electron microscopy. The reproductive structures of these genera are quite different from those of the *Arthrobotrys-Dactylella-Monacrosporium* complex.

6 Further studies to clarify the specific and generic delimitation

6.1 Cultural variability

A selection of the most suitable substrates to induce the typical development of morphological features is crucial for a taxonomic treatment.

6.1.1 *Effects of the substrate*
The nematode-trapping species of the *Arthrobotrys-Monacrosporium* complex are capable of growing on water agar, especially when supplemented with nematodes. On the other hand, as saprophytes, they readily grow on almost all kinds of artificial media, amongst which cornmeal (= maizemeal) agar has a long tradition since the studies of Drechsler.

There are numerous reports about the morphological deviations of nematode-trapping fungi due to cultivation on different media. Drechsler (1937) compared growth, conidiation, and conidial size of a species cultured on nematode-infested agar with the same species cultured on cornmeal agar. He found that network-forming species generally sporulate even better in pure culture. Also the morphology of the conidiophore might change depending on the substrate. *A. conoides*, *e.g.*, can produce in pure culture on CMA 5-10 additional conidial clusters through repeated elongation of the conidiophore [p. 24] instead of the single terminal head formed on wormy agar. *M. bembicodes* grows very slowly on CMA and hardly sporulates, in contrast to cultures on nematode-infested agar. The differences of cultivation are striking in *M. leptosporum*: the average length and width of conidia developed on nematode-infested agar reaches 53 x 4.6 μm whereas conidia from cornmeal agar, where reproduction usually is more copious, measure 73 x 5 μm.

Cooke and Dickinson (1965) compared conidia of *M. fusiforme* and *M. salinum* on nematode-infested rabbit dung agar (RDA) to those formed on Difco cornmeal agar (CMA). They were different in shape (*M. salinum*) and septation (*M. fusiforme)*, and in both species they varied in size. Conidia of *M. mutabile* markedly differed both in size and shape when grown in pure culture on cornmeal agar instead of a nematode-infested substrate (Cooke, 1969).

Matsushima (*e.g.* 1971, 1993) used different media, such as cornmeal agar supplemented with yeast extract (his CMA), with or without a sterilized piece of banana leaf, or V8 Juice agar (made from V8, 10 times diluted and neutralized). For some isolates he gave measurements of conidia originating from two different media, so that the cultural variability of the strain becomes obvious.

However, not all species or isolates react so strongly to the composition of the media as shown by Drechsler for *M. leptosporum*. In the present study (Table 2) the number of conidia per conidiophore, conidial size, and number of septa were recorded for four selected isolates (*M. haptotylum*, *M. elegans*, *M. lobatum*, and *M. thaumasium*) on two different media. All cultures were kept under the same conditions: at room temperature (about 23 ºC) under day light (in the laboratory). Water agar cultures were inoculated with pieces of agar originating from water agar cultures. Nematodes were added after two days of cultivation when the mycelium started to grow on the fresh agar plate. Measurements were made after seven days of cultivation (for *M. lobatum* and *M. thaumasium* after 11 days on WA plus nematodes because sporulation was slower). The number of conidia per conidiophore was determined after 14 days.

This experiment shows that the differences between nematode-infested cultures and pure cultures are conspicuous only in two of the four species: *M. lobatum* CBS 329.94 develops more slender conidia on nematode-infested WA and *M. thaumasium* CBS 320.94 develops much smaller conidia, which are sometimes only two-septate, in contrast to the regularly three-septate conidia formed on CMA:2.

It seems that not all species (isolates) are equally variable and the identity of a species is still recognizable on any of these media.

The question arises on which medium is the morphology most typical for these fungi. A natural appearance obviously results when the fungus is grown on a medium poor in nutrients (resembling soil or other substrata the fungi are isolated from) like WA to which nematodes have been added (an important source of nutrients under natural conditions). In this study another medium lacking soluble sugars, *viz.* half-strength cornmeal agar was preferred when measuring the conidial apparatus. The reason for this decision mainly lies in the greater practicability of axenic cultures and the experience that this medium in general produces a good sporulation without causing degeneration of the [p. 25] fungus. Half-strength cornmeal agar was preferred to a full-strength medium because less aerial mycelium was produced.

Table 2: Development of four species of *Monacrosporium* on WA plus nematodes and on CMA:2.

Strain	medium	no. conidia	conidial measurements	septa
CBS 325.94	WA + N	-12	31.5-39.5-47 x 8-10-11.5	4
M. haptotylum	CMA:2	-15	33-40-47 x 8-10-12	4
CBS 326.94	WA + N	1	45.5-51.5-58 x 16.5-20-23.5	3
M. elegans	CMA:2	1(3)	44.5-52.5-60 x 17.5-19.5-21	3
CBS 329.94	WA + N	1	37.5-47-56.5 x 8.5-99-10	3
M. lobatum	CMA:2	1	39.5-47-54 x 9.5-11-12.5	3
CBS 320.94	WA + N	-4	26.5-34.5-42 x 14.5-17-19.5	3 (2)
M. thaumasium	CMA:2	-9	35-44.5-53 x 18-21-24	3

6.1.2 *Effects of temperature and humidity*

When grown at temperatures other than at about 20-23 ºC, species (isolates) of the complex show the same trend as at room temperature (compare 6.2.1). The network-forming species also grow faster at 15 and 30 ºC than species with other types of trapping organ. In all network-forming species growth was faster when incubated at 30 than at 15 ºC. In contrast, the knob- and ring-forming species as well as non-predacious species grow better at 15 than at 30 ºC; many of them did not grow at all at 30 ºC. Not a single isolate grew at 35 ºC. The most thermotolerant were some isolates of *M. thaumasium*, growing at 33 ºC.

The literature contains some information about the preference of some nematode-trapping fungi for certain temperatures. *M. psychrophilum* favours low temperatures, as shown by Drechsler (1944 a) and confirmed by Rubner (1994), whereas *A. musiformis* is mainly isolated from warmer regions (Rubner, l.c.). Gray (1982) compared isolates of *M. ellipsosporum* and *M. cionopagum* (= *M. gephyropagum*) from the maritime Antarctica and from Britain; he found that the growth optimum of the isolates depended on their origin, the Antarctic isolates growing significantly better below 20 ºC, when compared with the temperate isolates.

In order to find out whether conidial size and septation are affected by the temperature of incubation, two isolates of *M. psychrophilum* and one of *M. elegans* were cultivated at 15 and 25 ºC. Twenty conidia from each plate were measured after 10 days (Table 3).

A slight difference was found between conidia developed at 15 and at 25 ºC. Conidia produced under warmer conditions were somewhat longer and narrower, [p. 26] therefore having a slightly higher length : width ratio, and there was a slightly higher proportion of conidia with two septa. However, these differences are not significant.

Table 3: Development of *M. elegans* (CBS 316.94) and *M. psychrophilum* (CBS 318.94, 319.94) at two different temperatures. Conidial length and width with standard deviation (s.d.), number of two-septate/three-septate conidia (Septa), and length : width ratio (l : w) were recorded.

Isolate	temp.	conidial size (µm)		septa	1 : w
CBS 316.94	15 ºC	43-46.5(s.d. 1.85)-49	x 17.5-21.5(s.d. 1.65)-23.5	3/17	2.16
	25 ºC	42-48.5(s.d. 2.95)-54	x 18-21(s.d. 1.80)-22	5/15	2.31
CBS 318.94	15 ºC	43-46.5(s.d. 2.05)-50.5	x 17.5-22.5(s.d. 1.66)-25	2/18	2.07
	25 ºC	42-47(s.d. 2.53)-53	x 17.5-21.5(s.d. 1.50)-23.5	6/14	2.19
CBS 319.94	15 ºC	39.5-45(s.d. 2.40)-49	x 22-23(s.d. 1.00)-25	4/16	1.96
	25 ºC	42-48(s.d. 3.25)-54	x 19-21(s.d. 1.70)-25	5/15	2.28

A pilot study with variation of the air humidity was carried out to assess effects of septa moisture on growth and sporulation. A desiccator containing different saturated salt solutions was used. K2CO3 yielded 45 %, NaCl 76 %, and plain water an almost 100 % air humidity. In addition, dry silica gel was used to create a very dry atmosphere. The Petri dishes with CMA:2 cultures facing upward were incubated without their lids in the desiccator for one week. The growth rate and sporulation capacity were measured or estimated, respectively. *A.oligospora* A.R. 936 and *M.parvicolle* A.R. 9310 showed exactly the same growth characteristics and no visible differences in sporulation under all conditions tested.

6.2 Additional, non-morphological tests

Six tests were applied to find non-morphological characters that might support the delimitation of genera. Though none of them was found to be discriminatory, they may serve to characterize the whole complex or parts of it.

6.2.1 *Colony growth rates*
The growth rates of nematode-trapping hyphomycetes are rather variable. It was shown that species (isolates) developing networks grow relatively fast, those forming stalked knobs, hyphal branches and unstalked knobs grow more slowly, and those with constricting rings are the slowest. The correlation between growth rate and trapping organ was already noticed by Cooke (1963) and later by Jansson (1982). Consequently, two ecological groups were distinguished. The first group comprises species with adhesive networks; they are fast-growing, good saprophytes, with a weak predacious activity. The second group comprises species with all other types of trapping organs; they are slow-growing, [p. 27] weak saprophytes and show higher predacious activities. Moreover, their trapping organs often develop spontaneously and need not be induced like the adhesive networks (Jansson, 1982). The results of the present study (Table 4) partly confirm Jansson's findings: the distinction between the two groups is quite sharp. The species are, therefore, primarily grouped according to their type of trapping organ and then according to their generic classification. The spontaneous formation of trapping organs of the second group, however, could not always be confirmed in the course of this revision.

Table 4: Species (isolates) with their growth rates (mm radius within 3 days, at room temperature)

Trapping mech.	species (strains)	radius
networks	*A. amerospora* (CBS 331.94)	12
	A. cladodes (A.R. 9331, A.R. 9335, A.R. 9337)	18, 17, 20
	A. musiformis (CBS 449.93)	17
	A. oligospora (CBS 337.94, 338.94)	22, 24
	A. robusta (CBS 339.94, 340.94)	18, 17
	A. superba (CBS 341.94)	17
	D. flagrans (CBS 342.94, 343.94)	18, 18
	M. elegans (CBS 299.94, A.R. 9229, CBS 316.94)	20, 20, 20
	M. psychrophilum (CBS 318.94, 319.94)	20, 20
	M. thaumasium (CBS 320.94, 322.94, 323.94, A.R. 9334)	20, 18, 20, 20

stalked knobs	*M. haptotylum* (CBS 325.94, 326.94, A.R. 9336)	6, 7, 7
	M. ellipsosporum (CBS 302.94, 303.94, 304.94)	7, 8, 9
hyphal branches	*M. gephyropagum* (CBS 308.94, 310.94, 311.94)	6, 6, 7
unstalked knobs	*M. lobatum* (CBS 329.94)	10
	M. parvicolle (CBS 312.94, 313.94, 314.94)	6, 6, 5
	M. phymatopagum (CBS 315.94, 317.94)	5, 5
constricting rings	*A. brochopaga* (CBS 332.94)	5
	A. dactyloides (CBS 333.94, 334.94, 335.94)	5, 6, 5

6.2.2 Cellulolytic activity

There are literature reports about the utilization of cellulose and the production of cellulases by a species of *Arthrobotrys* (*e.g.* Reese and Levinson, 1952; cited in Domsch *et al.*, 1980) or the copepod-trapping *Monacrosporium copepodii* (Barron, 1990). A general ability to decompose cellulose was also assumed for the predacious fungi since *Arthrobotrys*, *Dactylella,* and *Monacrosporium* had been isolated not only from soil, but also from leaf litter and dead standing plants (Rubner, unpubl. results).

Forty-four strains were tested. They were grown on cellulose agar until they reached about half the diameter of the Petri dish. Fungi with three-dimensional networks all gave positive results as well as the non-predacious species tested. In those with other trapping organs the outcome was sometimes equivocal. In a first test all five species [p. 28] forming constricting rings (*Arthrobotrys brochopaga*, *A. dactyloides*, *Monacrosporium doedycoides*, *M. effusum*, *M. polybrochum*) were negative. In subsequent tests, however, these strains seemed to degrade cellulose at least to some degree.

The following species (number of isolates in parentheses) tested showed a positive result: *Arthrobotrys amerospora*, *A. brochopaga*, *A. cladodes*, *A. conoides* (2), *A. dactyloides* (3), *A. javanica*, *A. musiformis*, *A. oligospora* (2), *A. scaphoides* (2), *A. vermicola*, *Dactylella cylindrospora*, *D. oviparasitica*, *D. oxyspora* (2), *D. rhopalota* (3), *D. spermatophaga*, *Duddingtonia flagrans* (2), *Monacrosporium haptotylum*, *M. doedycoides* (2), *M. drechsleri*, *M. effusum*, *M. ellipsosporum* (2), *M. gampsosporum*, *M. gephyropagum* (2), *M. parvicolle* (2), *M. phymatopagum* (2), *M. polybrochum*, *M. reticulatum*, and *M. thaumasium* (3).

6.2.3 Lignolytic activity

To detect lignolytic abilities, a phenoloxidase test was applied. Of the 30 strains tested, only two showed a positive result (*D. oviparasitica* CBS 347.85 and *M. effusum* CBS 774.84), three gave a weak colouring(*D. oxyspora* CBS 280.70, *M. arcuatum* CBS 174.89 and *M. phymatopagum* CBS 325.72), and all others were negative.

The non-predacious *D. oviparasitica* CBS 347.85 was isolated from the cysts of *Globodera rostochiensis* and *D. oxyspora* CBS 280.70 from an old stem of *Angelica archangelica*; the other three nematode-trapping isolates originate from soil (CBS 325.72 and CBS 774.84) and decaying leaves (CBS 174.89), and form different types of trapping organs.

6.2.4 Germination

The germination behaviour was studied in 14 strains, of which seven belong to *Monacrosporium*, five to *Arthrobotrys* and two to (non-predacious) *Dactylella*. Conidia from a well-sporulating CMA:2 culture were washed off with sterile tap water and transferred with a pipette to microscope slides. These slides (without cover slips) were kept for 48 hours in a moist chamber and checked on the first day every hour (eight times) for germination. All species tested formed germ tubes only from the basal (or parabasal) and apical (or penultimate) cells (Fig. 12). Even after 24 and 48 hours, none of the central cells germinated. No real difference was observed in the germination mode with regard to time, number of germ tubes and site of germination. One of the two *A. conoides* isolates tested germinated readily (A.R. 934, after two hours), the other (A.R. 9142) had not germinated after seven hours. The two strains of *M. thaumasium* (CBS 321.94 and 322.94) both germinated after about 4 hours.

It has been observed in other hyphomycetes that the middle cell of phragmosporous conidia usually do not produce germ tubes. It is difficult to say whether the adhesive knobs of *M. phymatopagum* are a sign of maturity or are part of the germination process. [p. 29]

Fig. 12.
Germinating conidia of:
a. *A. dactyloides;* b. *A. conoides;* c. *M. doedycoides;* d. *M. gampsosporum;* e. *M. thaumasium;* f. *M. phymatopagum;* g. the non-predacious *D. oxyspora.*[p. 30]

6.2.5 *Numbers of nuclei*

Nuclei were stained with DAPI. Most of the isolates investigated had multinucleate hyphal and/or conidial cells. If the conidial cells contained more than 5-10 nuclei as was usually observed with the enlarged middle cells of *Monacrosporium*, the numbers of nuclei could only be roughly estimated. Some conidial cells showed about 20 nuclei. The numbers of nuclei seem to be proportional to the volume of the cells. Some of the results of this preliminary study are listed below:

A. amerospora, CBS 331.94, amerosporous: conidia with about 12 nuclei.
A. conoides A.R. 9142, didymosporous: conidial cells variably multinucleate, *e.g.* 6 (basal cell)/ 20 (apical cell) nuclei.
Arthrobotrys sp., CBS 395.93, phragmosporous, (like all subsequent species); each of the four conidial cells with 1-4, mostly 2 nuclei.
Dactylella oxyspora, CBS 330.94: each of the four conidial cells with 1-4, mostly 2 nuclei.
D. rhopalota, CBS 845.70 and CBS 615.92: mycelial cells regularly with 1 nucleus.
M. elegans, L.P. 906: each of the four conidial cells multinucleate, *e.g.* 7 (basal cell) / 6 (parabasal cell) / >20 (middle cell) / 8 (apical cell).
M. doedycoides, CBS 175.55: mycelial cells multinucleate, 2-5 nuclei each.
M. gephyropagum, (isolate from G. Lysek) (often two-celled trapping organs in this isolate): each cell of the trapping organ with at least 2 nuclei, *e.g.* 2 (distal cell) / 3 (proximal cell), 2/2, 4/3, 3/3.

6.2.6 *Coenzyme Q*

The side chain length of coenzyme Q (ubiquinone) has been used for over three decades in the classification of fungi, mainly as a generic criterion. Some species of the *Arthrobotrys-Dactylella-Monacrosporium* complex were analysed in order to detect possibly different ubiquinone systems: *A. oligospora* (A.R. 9111), *M. haptotylum* (CBS 217.92), *M. gephyropagum* (CBS 587.91), and *D. rhopalota* (CBS 493.67) all showed predominantly Q-10(H2). These results confirm their relationship to the Ascomycetes (Kuraishi *et al.*, 1985). As the coenzyme Q was the same for all these rather divergent species, the study was discontinued.

6.3 Discussion

The additional tests did not yield any further criterion for a generic delimitation within the *Arthrobotrys-Monacrosporium* complex. This complex seems to be a rather homogeneous group of hyphomycetes, which may represent a mono- or paraphyletic group. The distinction of these two genera is retained here as a convenient practical solution to help in identification and delimit the group to be treated in this revision.

Fungal teleomorphs usually contain many more characters than anamorphs. As the characters associated with sexual reproduction are thought to be particularly stable, these perfect states or teleomorphs are preferred when constructing a natural system. As in the present case teleomorphs are usually unknown, I have tried to group the species of the *Arthrobotrys-Dactylella-Monacrosporium* complex with regard to their possible evolution. [p. 31]

A preliminary phylogenetic tree is presented here. The discovery of more teleomorph connections in *Arthrobotrys-* and *Monacrosporium* species or any molecular data will serve to evaluate these supposed relationships. The suggested phylogenetic tree is of hypothetical and speculative character, and no taxonomic or nomenclatural conclusions are drawn from it.

In predacious fungi the characters of the simple hyphae and reproductive structures (conidiophores and conidia) are scarce and do not vary very much in some groups. The trapping organs, however, are complex and (morphologically) stable (4.5, 4.6) and thus provide valuable criteria to elucidate relationships. These two sets of characters vary independently from each other, and one of them must be chosen as the primary criterion.

It is likely that more mutation steps are needed to modify a trapping organ fundamentally than to change the conidiophore tip or conidial shape and septation. Therefore, the types of trapping organs are used here as the primary criterion and a hypothetical development is assumed from adhesive knobs to adhesive networks or to constricting rings. In such a scheme, very similar conidial shapes have been reached convergently on different branches. As a consequence, the generic limits between *Arthrobotrys* and *Monacrosporium* are dissolved.

Figure 13 shows the suggested evolution of the predacious hyphomycetes from non-predacious ancestors and the presumed evolution of trapping organs. Predacity could have first be accomplished by morphologically unspecialized hyphae producing a substance to which the animals adhere. [Species of *Arthrobotrys* may also capture nematodes in an initial stage directly on the hyphae, before the loops of the three-dimensional networks are produced (G. Lysek, pers. comm.) or this may even be the sole capturing mechanism (Den Belder and Jansen, 1994).] *A. anomala* traps nematodes both by means of adhesive branches and networks (Barron and Davidson, 1972), *A. botryospora* captures the smaller nematodes by simple adhesive hyphae (Barron, 1979b). *Triposporina* and *Tridentaria* are also representatives of this primitive type of trapping. Apart from these, the least differentiated trapping devices are more or less globose sticky knobs which may have evolved in two or three directions: they may have become elongated and proliferated (hyphal outgrowths), then have developed bridges between the outgrowths (scalariform or two-dimensional networks) and finally developed additional loops (three-dimensional networks). On the other side, the knobs were extended by stalks (stalked knobs). The derivation of non-constricting and constricting rings is the least plausible step of evolution. The simultaneous occurrence of (long) stalked knobs and
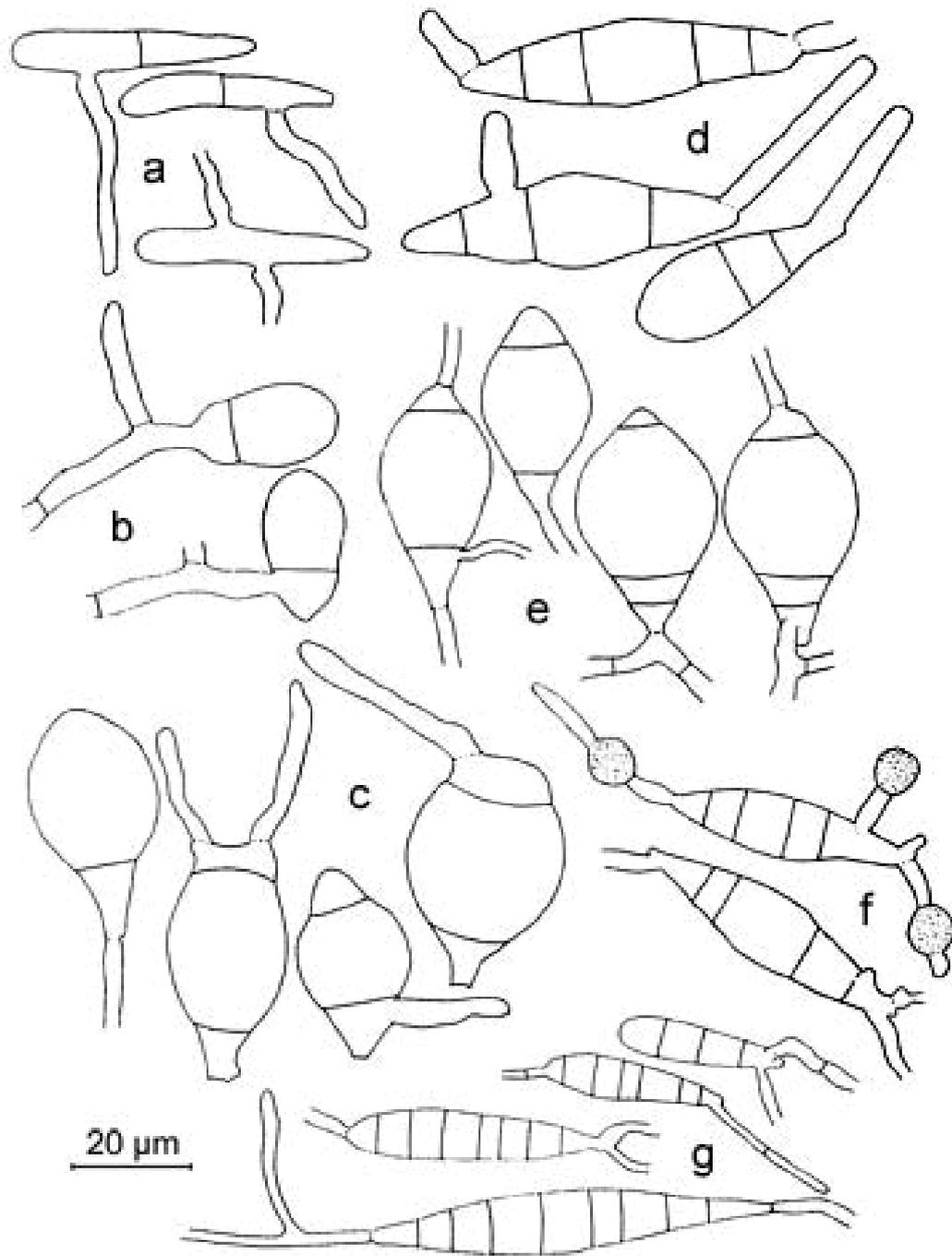
Fig. 12.
Germinating conidia of:
a. *A. dactyloides*,
b. *A. conoides*,
c. *M. doedycoides*,
d. *M. gampsosporum*,
e. *M. thaumasium*,
f. *M. phymatopagum*,
g. the non-predacious *D. oxyspora*.
[p. 30]

non-constricting rings in several species might be a hint for a homology of the two types of trapping organs.
It is certainly a long way from the non-constricting to the constricting rings. However, there are some similarities between the two: they both lack adhesive material characteristic for all other types of trapping organs; they are both stalked and their rings consist of three cells. The relationship is possibly illustrated by a degenerated strain of *M. doedycoides* (CBS 175.55) which produced non-inflatable ring cells borne on a stalk; these ring cells (more than three) grew in a coil and were not functional in trapping nematodes (Fig. 9). [p. 32]

Fig. 13.
Hypothetical development of the mode of life of hyaline, phragmosporous hyphomycetes (base of tree) and development of specialized trapping organs (upper part of tree) for the capture of nematodes. [p. 33]

Fig. 14.
Hypothetical development of the conidiophore tip and conidia (reduction of size and septa) among the species of *Arthrobotrys* and *Monacrosporium* forming constricting rings. [p. 34]

Fig. 15.
Hypothetical development of the conidiophore tip and conidia (reduction of size and septa) among the network-forming species of *Arthrobotrys* and *Monacrosporium*. [p. 35]

Constricting rings and three-dimensional networks are the most derived (ecologically most successful and most frequent) types of trapping organs. In the Figures 14 and 15 representatives of both groups are drawn together with conidiophore types and associated conidial forms. The latter were arranged in a presumptive phylogenetical order, again mainly based on the complexity of these structures and on indications obtained from non-predacious *Dactylella* species. These and non-predacious species of *Dactylella* as well as knob-forming (plesiomorphic) species of *Arthrobotrys* and *Monacrosporium* all have simple conidiophores and multiseptate conidia. Thus, arthrobotryoid conidiophores and didymosporous or amerosporous conidia appear to be apomorphic character states. Structures linking the most primitive and the most derived type of conidiophore would be the conidiophores with denticles and geniculate conidiophores.

Typical representatives of *Monacrosporium* and *Arthrobotrys* can have either types of trapping organs.

Even if order (sequence) and polarity (developmental direction) of the characters are questioned, and the outlined phylogenetic trees (Figs 13, 14 and 15) are not at all certain, it can be stated that the *Arthrobotrys* type (with its arthrobotryoid conidiophores and the typically didymosporous conidia) occurs in at least two different groups of predacious species (*e.g. A. anchonia* in the group of constricting ring formers and *A. cladodes* in the group of network formers). This means that the *Arthrobotrys* type has evolved at least twice (polyphyletic) or has evolved convergently.

A taxonomic and nomenclatural consequence of this fact would be a merging of all predacious hyphomycetes with ascomycete relationship and with a special type of trapping organ in one genus, stressing the close relationship of all these taxa. Alternatively, if the differences between the trapping organs is stressed, a generic delimitation could be made on the basis of the trapping organs.

As long as any new indications from teleomorph connections are lacking and no other new characters are found to support such a construction, no name changes are made.

The line between nematode-capturing and non-predacious fungi appears to be rather sharp. *Dactylella*, so far poorly delimited, can be confined to the latter, and all nematophagous species formerly classified in *Dactylella* are transferred to *Monacrosporium*. [p. 36]

7 The generic names used for hyphomycetes of the *Arthrobotrys-Dactylella-Monacrosporium* complex

(Accepted genera are printed in **bold face**).

Anulosporium Sherb. - Mycologia **25**: 262. 1933.
        Type species: *Anulosporium nematogenum* Sherb.
The genus was erected for fungi with non-constricting rings, which were erroneously interpreted as spores. As no conidia were described, it is not possible to decide whether a species of *Arthrobotrys* or *Monacrosporium* was
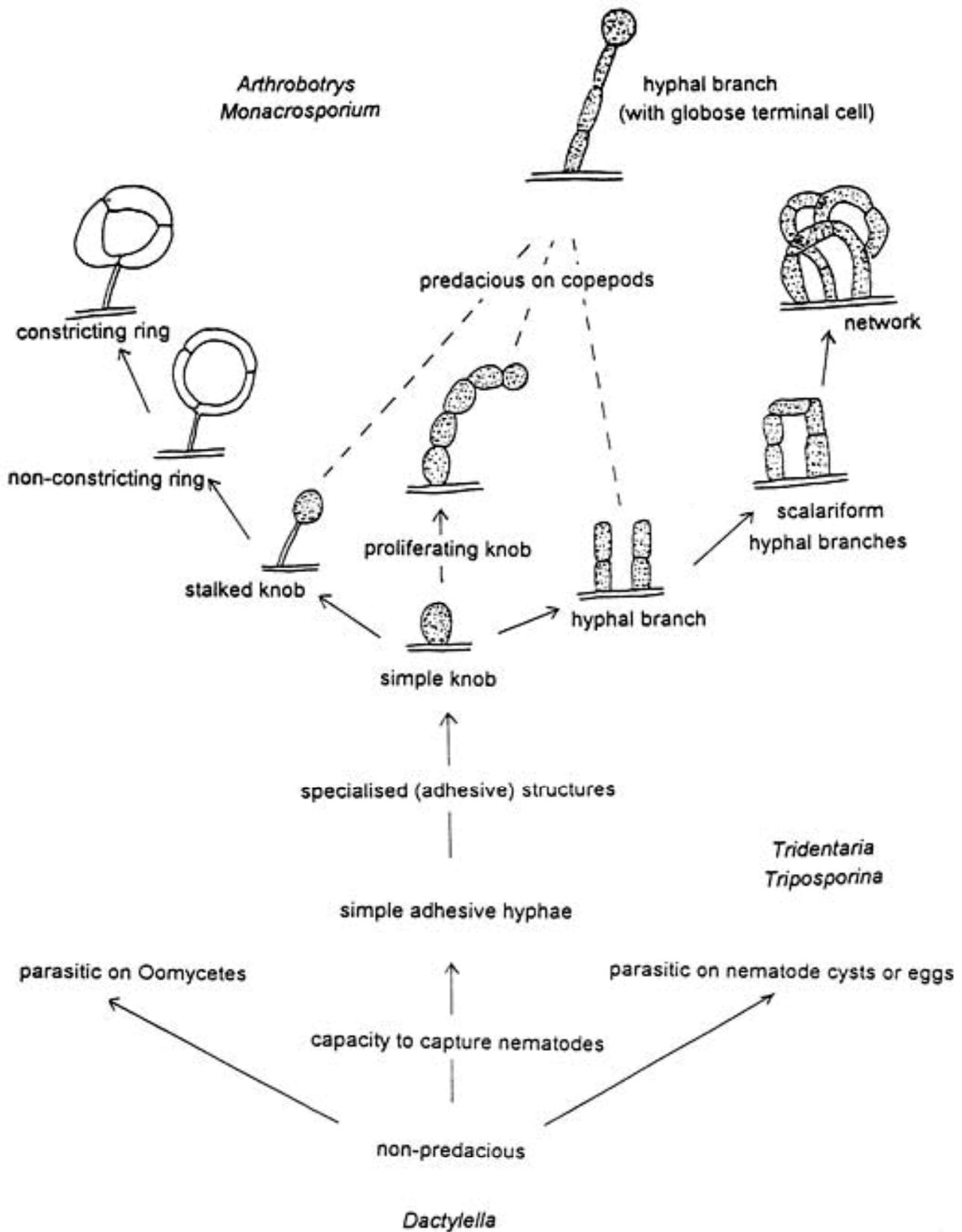
Fig. 13. Hypothetical development of the mode of life of hyaline, phragmosporous hyphomycetes (base of tree) and development of specialized trapping organs (upper part of tree) for the capture of nematodes. [p. 33]

Fig. 14. Hypothetical development of the conidiophore tip and conidia (reduction of size and septa) among the species of *Arthrobotrys* and *Monacrosporium* forming constricting rings. [p. 34]

A. amerospora

retrogressive formation of conidia

A. cladodes

reduction of conidiophore tip to a single terminal node

A. musiformis

A. oligospora

condensation of conidial nodes

A. vermicola

in several directions

sympodial elongation of the geniculate conidiophore tip
in one direction

(candelabrelloid
conidiophore tip)

M. eudermatum

elongation of the the denticles and proliferation
(geniculate conidiophore tip)

M. megalosporum

branching of conidiophore tip (denticles)

M. multiforme
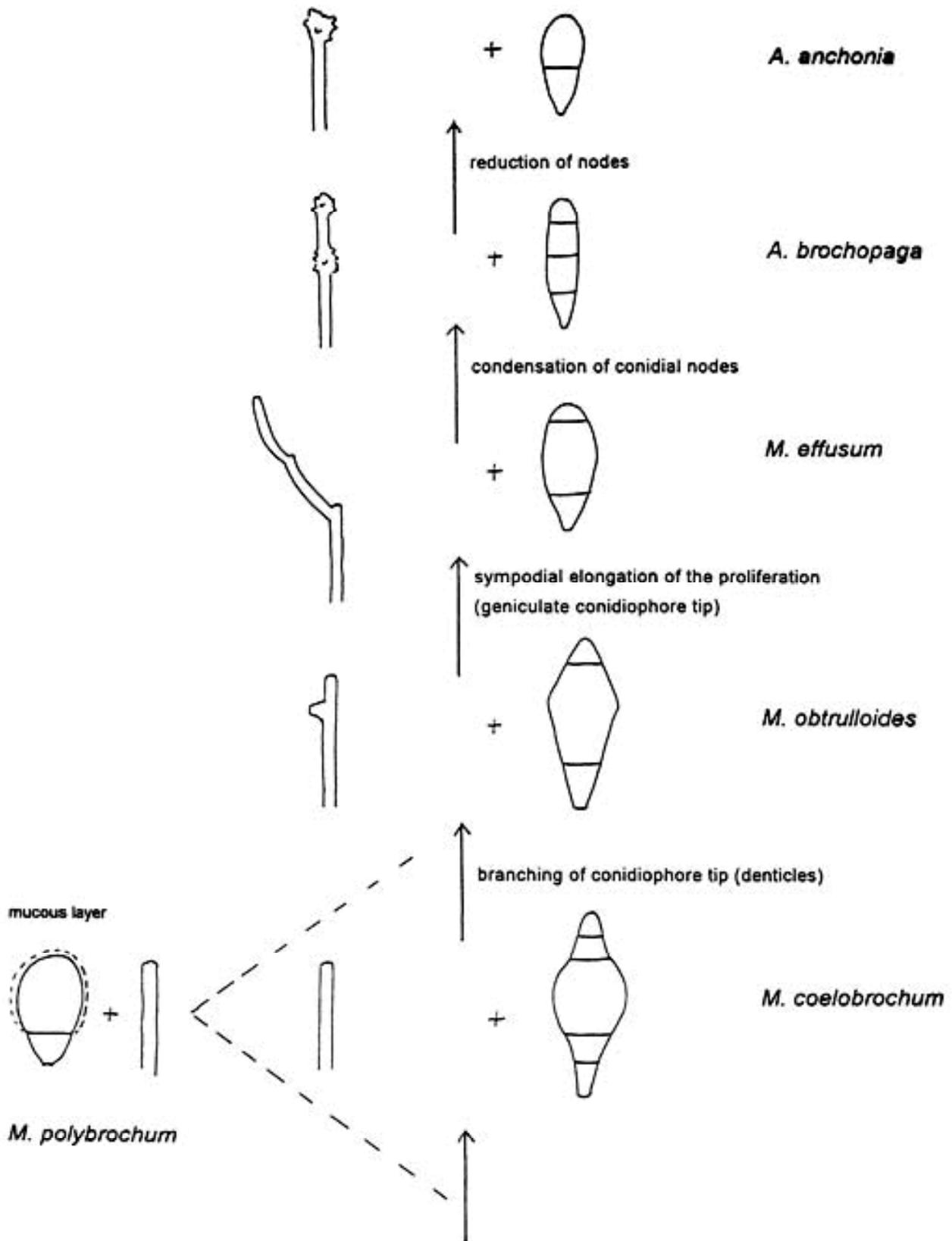
Fig. 15. Hypothetical development of the conidiophore tip and conidia (reduction of size and septa) among the network-forming species of *Arthrobotrys* and *Monacrosporium*. [p. 35]

concerned, and the genus remains doubtful.

Arthrobotrys Corda - Prachtflora europäischer Schimmelbildungen: 43. 1839.
Type species: *Arthrobotrys superba* Corda.
Some important taxonomic treatments: Haard (1968); Jarowaja (1970); Schenck *et al.* (1977); van Oorschot (1985).
    = *Didymozoophaga* Soprunov & Galiulina 1951
    = *Candelabrella* Rifai & R.C. Cooke 1966
    = *Dactylariopsis* Mekht. 1967
    = *Geniculifera* Rifai 1975
    = *Nematophagus* Mekht. 1975
    = *Woroninula* Mekht. 1979.

Candelabrella Rifai & R.C. Cooke - Trans. Br. mycol. Soc. **49**: 160. 1966.
Type species: *Candelabrella javanica* Rifai & R.C. Cooke.
    = **Arthrobotrys**, fide Barron (1968), Schenck *et al.* (1977), van Oorschot (1985).

Dactylaria Saccardo - Michelia **2**: 20. 1880.
    Type species: *Dactylaria purpurella* (Sacc.) Sacc. 1886 • *Acrothecium purpurellum* Sacc. Some important taxonomic treatments: Bhatt and Kendrick (1968); de Hoog and von Arx (1973); Matsushima (1975); Ellis (1976); de Hoog (1985).
Representatives of the genus have pigmented conidiophores and (sub-)hyaline conidia borne on slender denticles. All nematode-trapping species have been excluded from *Dactylaria*.

Dactylariopsis Mekhtieva - Mikol. Fitopatol. **1**: 278. 1967.
    Type species: *Dactylariopsis brochopaga* (Drechsler) Mekht. • *Dactylaria brochopaga* Drechsler 1937 • *Arthrobotrys brochopaga* (Drechsler) S. Schenck, W.B. Kendr. & Pramer.
        = **Arthrobotrys**
The type species with its arthrobotryoid conidiophore tips bearing conidia in whirls, is a typical representative of *Arthrobotrys* although conidia are usually three-septate.

Dactylella Grove - J. Bot. **22**: 199. 1884.
    Type species: *Dactylella minuta* Grove.
Some important taxonomic treatments: Lindau in Rabenhorsts Kryptogamenflora **8**: 411 (1905); Drechsler (*e.g.* 1937, pp. 447-552); Arnaud (1952); Yadav (1960); Subramanian (1963); Cooke and Dickinson (1965). [p. 37]
    = *Drechsleromyces* Subram. 1977
    = *Gangliophragma* Subram. 1977.
D. minuta is believed to be a non-nematophagous fungus. All nematophagous species hitherto described in the genus differ from the type species by generally longer conidiophores, less densely and mostly inequidistantly septate conidia, which are mostly top-shaped. Hence, they are all transferred to *Monacrosporium*.

Dactylellina Morelet - Bull. Soc. Sci. Nat. Archéol. Toulon Var **178**: 6. 1968.
    Type species: *Dactylellina leptospora* (Drechsler) Morelet • *Dactylella leptospora* Drechsler.
     • *Dactylosporium* Mekht. [non Harz]
        = **Monacrosporium**
The genus is regarded as superfluous as the type species is a typical representative of *Monacrosporium* (see *Dactylosporium Mekht.*).

Dactylina G. Arnaud - Bull. trimest. Soc. mycol. Fr. **68**: 181. 1952 [*nom. inval.*, Arts. 36, 37 ICBN].
Dactylina G. Arnaud ex Subram. - J. Indian bot. Soc. **42**: 291. 1963 [*nom. illeg.*, Art. 53 ICBN].
    Type species: *Dactylina tylopaga* (Drechsler) Subram. • *Dactylella tylopaga* Drechsler.
Replaced by **Lactydina**.

Dactylium Nees, Das System der Pilze und Schwämme: **58**. 1817 : Fries, Syst. mycol. 3: 382. 1832.
    Type species: *Dactylium candidum* Nees • *Dactylaria candida* (Nees : Fr.) Sacc., *nom. dubium* fide Barron (1968).
The type species *D. candidum* is of doubtful identity, although an apparently similar predacious fungus was redescribed by Drechsler (1937) as *Dactylaria candida*. If this were accepted as a neotypification, the genus *Dactylium* would have to replace *Monacrosporium*. Therefore formal rejection of *Dactylium candidum* is proposed by Gams and Rubner (1996).

Dactylium Sacc. - Sylloge Fungorum **4**: 188-190. 1886 [*nom. illeg.*, Art. 53 ICBN].
    Type species: *Dactylium dendroides* (Bull. : Fr.) Fr. • *Cladobotryum dendroides* (Bull. : Fr.) W. Gams & Hoozem.
Some important taxonomic treatments: Lentz (1965); Gams and Hoozemans (1970); de Hoog (1985); Helfer (1991); Samuels and Rogerson (1993).
An overview on the name history of *Dactylium* was given by Lentz (1965). Nomenclatural confusion arose when Saccardo (1886) introduced *Dactylium* Sacc. by excluding the type, *D. candidum* Nees to *Dactylaria* in 1882, and when Clements and Shear (1931) consequently cited *Dactylium dendroides* (Bull. : Fr.) Fr. as the type species of *Dactylium*. Therefore Lentz (1965) proposed *Dactylium* Sacc. for conservation because of the established usage.

This proposal was rejected by the Committee for Fungi and Lichens, because *Cladobotryum* was available for the mycophilic fungi in question (Donk, 1968).

Dactylosporium Mekht. - Mikol. Fitopatol. **1**: 278. 1967 [non Harz 1871], *nom. illeg.*, Art. 53 ICBN. [p. 38]
    Type species: *Dactylosporium leptosporum* (Drechsler) Mekht. • *Dactylella leptospora* Drechsler • *Monacrosporium leptosporum* (Drechsler) A. Rubner (see p. 79).
Replaced by *Dactylellina* Morelet 1968 and *Kafiaddinia* Mekht. 1978.
    = **Monacrosporium**
The genus was segregated from *Dactylella* because of conidiophores (with denticles) bearing conidia in a capitate arrangement, and predacious activity. These are characters regarded as characteristic of *Monacrosporium*.

Didymozoophaga Soprunov & Galiulina - Mikrobiologiya **20**: 493. 1951 [*nom. inval.*, Art. 36 ICBN].
    Type species: *Didymozoophaga superba* (Corda) Soprunov & Galiulina • *Arthrobotrys superba* Corda.
    = **Arthrobotrys**, fide Schenck *et al.* (1977), Domsch *et al.* (1980), Van Oorschot (1985).

Drechslerella Subram. - J. Indian bot. Soc. **42**: 299. 1963.
Type species: *Drechslerella acrochaeta* (Drechsler) Subram. • *Dactylella acrochaeta* Drechsler.
    = **Monacrosporium**, fide Liu & Zhang (1994).
The conidial appendices described by Drechsler for *D. acrochaeta* are interpreted as germ tubes and have no taxonomic significance.

Drechsleromyces Subram. - Kavaka **5**: 93. 1977.
    Type species: *Drechsleromyces atractoides* (Drechsler) Subram. • *Dactylella atractoides* Drechsler.
    = **Dactylella**
The type species is a typical representative of *Dactylella* with clavate to fusiform, equidistantly septate conidia, and a non-predacious mode of life.

Duddingtonia R.C. Cooke - Trans. Br. mycol. Soc. **53**: 316. 1969.
    Type species: *Duddingtonia flagrans* (Dudd.) R.C. Cooke • *Trichothecium flagrans* Dudd. This unispecific genus is distinct because of the mode of conidiogenesis (conidia formed at the conidiophore apex and slightly below without being borne on pronounced denticles) and the conspicuous production of chlamydospores.

Gangliophragma Subram. - Kavaka **5**: 94. 1977.
    Type species: *Gangliophragma rhopalota* (Drechsler) Subram.• *Dactylella rhopalota* Drechsler.
    = **Dactylella**
Subramanian erected the genus for species of *Dactylella* with sympodially proliferating conidiophores and gangliar (= broadly attached) conidia. The type species is, however, a typical representative of *Dactylella*, often mistaken for *D. minuta*, and non-predacious.

Genicularia Rifai & R.C. Cooke - Trans. Br. mycol. Soc. **49**: 153. 1968 [non *Genicularia* Rouss. ex Desv. 1808, non de Bary 1858], *nom. illeg.*, Art. 53 ICBN.
    Type species: *Genicularia cystosporia* (Dudd.) Rifai & R.C. Cooke • *Trichothecium cystosporium* Dudd.
Replaced by *Geniculifera* Rifai (1975). [p. 39]

Geniculifera Rifai - Mycotaxon **2**: 214. 1975.
    Type species: *Geniculifera cystosporia* (Dudd.) Rifai • *Trichothecium cystosporium* Dudd.
• *Arthrobotrys cystosporia* (Dudd.) Mekht.
    = **Arthrobotrys**
The genus was erected for species with a geniculate conidiophore, bearing one- to many-septate conidia. According to Schenck *et al.* (1977), its segregation from *Arthrobotrys* is not justified. The geniculate conidiophore is regarded here as a progression from a denticulate conidiophore. As can be seen within one species (*e.g.* **M. psychrophilum**), the conidiophore tip may either bear a single conidium at the tip or additional conidia on perpendicular branches or on geniculate branches.

Golovinia Mekht. - Mikol. Fitopatol. **1**: 275. 1967.
    Type species: *Golovinia bembicodes* (Drechsler) Mekht. • *Dactylella bembicodes* Drechsler • *Monacrosporium bembicodes* (Drechsler) Subram.
    = **Monacrosporium**, fide Liu and Zhang (1994).
The genus was erected by Mekhtieva for species with a single conidium on the tip of an erect conidiophore or in capitate arrangement (but not in arthrobotryoid clusters). It comprises species with didymosporous as well as phragmosporous, more or less spindle-shaped conidia. In 1979 Mekhtieva grouped almost all the species which are included here in *Monacrosporium* in *Golovinia* and *Dactylella* sensu Mekhtieva. The genus *Golovinia* is regarded as superfluous.

Kafiaddinia Mekht. - Mikol. Fitopatol. **12**: 8. 1978, a *nom. nov.* for *Dactylosporium* Mekht.

Type species: *Kafiaddinia fusarispora* Mekht. = *Monacrosporium leptosporum* (Drechsler) A. Rubner.
= **Monacrosporium**
As is discussed on p. 79, *K. fusarispora* is regarded as a synonym of *M. leptosporum*.

Lactydina Subram. - Kavaka **5**: 95. 1977, a *nom. nov.* for *Dactylina* Arnaud ex Subramanian 1963.
Type species: *Lactydina tylopaga* (Drechsler) Subram. • *Dactylella tylopaga* Drechsler. *L. tylopaga* with its appendages on the apical cells of the two-celled conidia is not representative of *Dactylella* or *Monacrosporium*. The erection of a separate genus seems to be appropriate (see also p. 120).

Laridospora Nawawi - Trans. Br. mycol. Soc. **66**: 344. 1976.
Type species: *Laridospora appendiculata* (Anastasiou) Nawawi • *Dactylella appendiculata* Anastasiou = *Monacrosporium tentaculatum* A. Rubner & W. Gams (p. 97).
= **Monacrosporium**
With its spindle-shaped conidia and the predacious activity, the type species is a typical representative of *Monacrosporium*, although its ecology (aquatic) and the conidial appendages connected with this habitat, are unusual for the genus.

Monacrosporiella Subram. - Kavaka **7**: 94. 1977.
Type species: *Monacrosporiella megalospora* (Drechsler) Subram. • *Dactylella megalospora* Drechsler • *Monacrosporium megalosporum* (Drechsler) Subram.
= **Monacrosporium** [p. 40]

Subramanian (1977) erected the genus for representatives with simple conidiophores, rarely branched at the tip and top-shaped conidia with a distinct basal hilum. The type species is a typical representative of *Monacrosporium*.

Monacrosporium Oudem. - Ned. kruidk. Archf, Ser. **2**,4: 250. 1885.
Lectotype species: *Monacrosporium elegans* Oudem., designated by Clements and Shear (1931), and also by Subramanian (1963).
Some important taxonomic treatments: Subramanian (1963); Cooke and Dickinson (1965); Cooke (1967 a); Liu and Zhang (1994).
= *Drechslerella* Subram. 1963
= *Golovinia* Mekht. 1967
= *Monacrosporiella* Subram. 1977
= *Kafiaddinia* Mekht. 1978.

Nematophagus Mekht. - Mikol. Fitopatol. **9**: 150. 1975.
Type species: *Nematophagus azerbaidzhanicus* Mekht. • *Arthrobotrys azerbaidzhanica* (Mekht.) Oorschot.
= **Arthrobotrys**
As can be seen from Mekhtieva's (1979) drawing, *N. azerbaidzhanicus* has arthrobotryoid conidiophore tips and fits the concept of *Arthrobotrys*.

Trichothecium Link - Mag. Ges. naturf. Freunde Berlin **3**: 18. 1809 : Fr. - Syst. mycol. **3**: 382. 1832.
Type species: *Trichothecium roseum* (Pers. : Fr.) Link.
This genus is characterized by very long, unbranched conidiophores and retrogressive formation of two-celled, thick-walled conidia. The three nematophagous species described in *Trichothecium* do not fulfil these criteria; they have been transferred to *Arthrobotrys* (*A. inaequalis)*, *Duddingtonia* (*D. flagrans)*, and *Monacrosporium* (*M. polybrochum*), respectively.

Woroninula Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 109. 1979.
Type species: *Woroninula polycephala* (Drechsler) Mekht. • *Dactylaria polycephala* Drechsler • *Arthrobotrys polycephala* (Drechsler) Rifai.
= *Monacrosporium*, fide Liu and Zhang (1994)
= **Arthrobotrys**
With its intercalary and terminal conidial whirls, the type species is a good representative of *Arthrobotrys*, although conidia are multiseptate. [p. 41]

8 Keys to genera and species

8.1 Key to the nematode-trapping genera of hyphomycetes and some similar genera

1 Conidiophores with swollen fertile nodes (arthrobotryoid); conidia one- or two-celled   *Arthrobotrys*

[If conidiogenous denticles are very narrow and mode of life mycoparasitic, cf. *Gonatobotrys*]

1* Conidiophores lacking swollen nodes, bearing a single conidium at the apex or additional conidia on perpendicular denticles arising further down the conidiophore; conidia mostly with more than one septum ... 2

2 Conidia two-celled ... 3

2* Conidia more than two-celled ... 4

3 Conidia arising on long denticles ... *Arthrobotrys*

3* Conidia produced on the apex of conidiophores, usually without forming discrete denticles ... *Duddingtonia*

4 Parasitic on oogonia of Oomycetes or on nematode cysts, or merely saprophytic; conidiophores rather short ... *Dactylella*

4* Predacious on nematodes or copepods (besides saprophytic mode of life) ... 5

5 Differentiated organs of capture present, either formed spontaneously or after induction with nematodes (or copepods, other animals, or chemical stimulus); conidia mostly top-shaped, spindle-shaped or sometimes clavate ... *Monacrosporium*

5* No trapping organs present; nematodes caught by adhesion to undifferentiated hyphae ... 6

6 Conidia compact, polyhedric with blunt projections; septa in several planes ... *Triposporina*

6* Conidia trident-like, elongated ... *Tridentaria*

8.2 Keys to the species of *Monacrosporium*, primarily based on the type of trapping organ

1 Trapping organ consisting of a three-celled ring borne on a stalk; when stimulated, e. g. by nematodes or by pressure, the ring cells inflate: constricting ring ... **Key A**

1* Trapping organ not a constricting ring ... 2

2 Trapping organ one- to multicellular, covered with an adhesive substance to which nematodes adhere; not a stalked ring ... 3

2* Trapping organ a non-constricting ring, three-celled and borne on a slender stalk; often accompanied by another type of trapping organ (long-stalked knob) [p. 42] ... **Key C**

3 Multicellular meshes forming a three-dimensional adhesive trapping organ: network ... **Key B**

3* Trapping organ not a three-dimensional network ... 4

4 Trapping organ consisting of elongated, often two-celled adhesive hyphal branches, which are often connected, scalariform ... **Key D**

4* Trapping organ of other type, mostly consisting of or bearing an adhesive knob ... 5

5	Trapping organ a stalked knob; sometimes accompanied by non-constricting rings	**Key C**
5*	Trapping organ an unstalked knob, often proliferating to unbranched, multicellular structures	**Key E**

Key A (species with constricting rings)

1	Conidia 1- or 2-septate	2
1*	Conidia more than 2-septate	8
2	Conidia regularly 1-septate, the apical cell covered with a mucous layer	*M. polybrochum*
2*	Conidia generally 2-septate	3
3	Conidia spindle-shaped or top-shaped	4
3*	Conidia ellipsoid or cylindrical with rounded ends	6
4	Conidia biconical, spindle-shaped; width about 14 µm	*M. obtrulloides*
4*	Conidia top-shaped or broadly spindle-shaped, average width around 20 µm	5
5	Conidia with a rather convex outline in the basal part; conidiophore tip not regularly swollen	*M. acrochaetum*
5*	Conidia with a conspicuously concave outline in the basal part; conidiophore tip regularly swollen (about 4 µm wide)	*M. doedycoides*
6	Only one type of conidia formed, conidia sometimes curved, not exceeding 16.5 µm in width	*M. stenobrochum*
6*	Two types of conidia formed, *i.e.* micro- and macroconidia or conidia very heterogeneous; conidia straight	7
7	Microconidia borne on short microconidiophores with a geniculate rachis, 1-septate, not exceeding 8 µm in width; catenate chlamydospores, regularly present	*M. heterosporum*
7*	Conidia of the smaller type not borne on a geniculate rachis, 10-15 µm wide; no chlamydospores known	*M. effusum*
8	Conidia mostly 4-septate	9
8*	Conidia mostly 3-septate [p. 43]	10
9	Conidia on average 46 µm long, not exceeding 55 µm	*M. aphrobrochum*
9*	Conidia longer (average 54 µm, reaching up to 64 µm), apical and basal cell protracted	*M. coelobrochum*
10	Conidia almost spherical and very large, 38-60 x 30-38 µm	*M. turkmenicum*
10*	Conidia top-shaped or spindle-shaped, not exceeding 24 µm in width	11
11	Conidial length 34-48 µm	*M. bembicodes*
11*	Conidial length 50-65 µm	*M. inquisitor*

Key B (species with adhesive networks)

1 Conidia very long, often around 100 µm   2

1* Conidia not exceeding 60-85 µm in length   3

2 Conidia sometimes branched, the branches measuring 14-95 x 5-12.5 µm   *M. iridis*

2* Conidia never branched; conidial septa often conspicuously inequidistant   *M. multiforme*

3 Conidia produced on the conidiophore tip in groups (up to 8 conidia); conidia slender (7-16 µm), often curved; microconidia often present, nonseptate   *M. gampsosporum*

3* The above characters not present in combination   4

4 Conidia generally 4-septate   5

4* Conidia not more than 3-septate   7

5 Conidia up to 85 µm in length, up to 25 µm in width; chlamydospores often present   *M. reticulatum*

5* Conidia not exceeding 75 µm in length   6

6 Conidia with variable number of septa (2-5, but mostly 4), conidial measurements 40-75 x 18-35 µm   *M. megalosporum*

6* Conidia rather constantly 3(-4)-septate, somewhat smaller, measuring 46-71 x 21-29 µm   *M. psychrophilum*

7 Conidia broad, almost globose, length : width ratio about 1.5, conidial width 19-23-28 µm   *M. eudermatum*

7* Conidia narrower, length : width ratio above 2   8

8 Conidia in groups of at least 3, sometimes up to 10 conidia on the conidiophore tip, borne on small denticles; conidia measuring 34-44-50 x 16-20-22.5 µm; chlamydospores often present   *M. thaumasium*

8* Conidia not in a terminal head, but often a few (1-3) additional conidia borne on small denticles lower down the conidiophore; chlamydospores not known [p. 44]   9

9 Conidia spindle-shaped, often up to 60 x 19 µm, regularly 3-septate   10

9* Conidia more ellipsoid than spindle-shaped, hardly exceeding 17.5 µm in width, varying in the number of septa (1-3)   11

10 Conidia with a distinctly inflated median cell, the parabasal and basal cells narrowly protruded into a tail, on average 52 x 20 µm   *M. elegans*

10* Conidia with a less distinctly inflated median cell, gradually tapering towards the ends; conidia somewhat larger, average width around 25 µm   *M. psychrophilum*

11 Conidia (from nematode-infested agar) up to 50 x 17.5 µm, mainly 2-septate   *M. fusiforme*

11* Conidia (from nematode-infested agar) up to 52.5 x 20 µm, mainly 3-septate   *M. salinum*

Key C (species with stalked knobs and/or non-constricting rings)

1	Stalks supporting the knobs long and slender, up to 15 (-35) µm long and 1-2 µm wide; non-constricting rings also borne on such slender stalks, sometimes (solely) present in the culture	2
1*	Stalks more stout, not exceeding 10 µm in length, 2-3 µm wide; never accompanied by non-constricting rings	4
2	Conidia very long and slender, not exceeding 5 µm in width; primary conidia 5-15-septate, secondary conidia 3-8-septate	*M. leptosporum*
2*	Conidia spindle-shaped, always wider than 5 µm, mostly 4-septate	3
3	Conidiophores bearing conidia in groups of 3-10 on the tip; average conidial width 8-9.5 µm	*M. haptotylum*
3*	Conidiophore usually with a single conidium on the tip; average conidial width 11.5 µm	*M. lysipagum*
4	Conidia regularly 4-septate	5
4*	Conidia usually 3-septate	7
5	Stalks supporting the knobs regularly two-celled, frequently branched near the base	*M. mutabile*
5*	Stalks not branched at the base	6
6	Conidia 40-49-60 long and up to 18 µm wide	*M. phymatopagum*
6*	Conidia 40-44-50 long and up to 16 µm wide	*M. ellipsosporum*
7	Conidia with a blunt apex, on average 35 x 11 µm, sometimes 4-septate	*M. mammillatum*
7*	Conidia with a more arcuate apex, on average 40 x 13 µm [p. 45]	*M. drechsleri*

Key D (species with hyphal branches)

1	Hyphal branches mostly two-celled, often forming bridges to each other; conidia broadly spindle-shaped, up to 60 µm long	*M. gephyropagum*
1*	Hyphal branches several-celled, very slender, sometimes ending with a globose knob, trapping copepods; conidia narrowly spindle-shaped, up to 97 µm long	*M. copepodii*

Key E (species with unstalked knobs which often proliferate)

1	Trapping organ unicellular, more or less elongate (16-85 x 9-10 µm); conidia 20-30 µm wide	*M. robustum*
1*	Trapping organs globose; conidia not exceeding 18 µm in width	2
2	Knobs not proliferating; conidia up to 60 µm long and up to 18 µm wide	*M. phymatopagum*
2*	Knobs often proliferating to form several-celled arches or rings; conidia not exceeding 55 x 15 µm	3
3	Conidia slender, 4-6 µm wide	*M. arcuatum*
3*	Conidia more than 8 µm wide	4

4 Conidia spindle-shaped, (3-)4-septate	*M. parvicolle*
4* Conidia more or less cylindrical, regularly and equidistantly 3-septate [p. 46]	*M. lobatum*

9 Descriptions of the species of *Monacrosporium*

Under *published descriptions* only those papers are cited that contain additional data and do not only copy parts of the protologue.

Measurements copied from Drechsler's original descriptions were taken from pure cultures on cornmeal agar, unless otherwise indicated. They express the range and the arithmetic means. Own measurements are all taken from cultures on CMA:2 and expressed in the same way.

The rate of growth of a colony is not indicated here, though it is characteristic for a species. Growth rates are related to the type of trapping organ (see Chapter 6.2.1, p. 26-27).

All scale bars in the figures correspond to 10 µm, unless otherwise indicated.

1. Monacrosporium acrochaetum (Drechsler) R.C. Cooke - Fig. 16.

Dactylella acrochaeta Drechsler - Mycologia **44**: 541. 1952 • *Drechslerella acrochaeta* (Drechsler) Subram. - J. Indian bot. Soc. **42**: 299. 1963• *Monacrosporium acrochaetum* (Drechsler) R.C. Cooke - Trans. Br. mycol. Soc. **50**: 317. 1968 • *Golovinia acrochaeta* (Drechsler) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 138. 1979.

Typification: Iconotype (Mycologia **44**: 535, 537, 539).

Published descriptions: Gray (1984).

Characteristics (after Drechsler, 1952)**:** Conidiophores (75-)325-450(-475) µm high, sometimes slightly inflated at the tip, bearing a single conidium. Conidia usually broadly fusiform, 30-35.3-42 x 13.2-19.5-22.6 µm, commonly two-septate. Chlamydospores yellowish, formed through induration of 1-12 hyphal or 1-3 conidial cells (at least the middle cell), the former type measuring 7-35 x 4-6 µm or, if subglobose, 10-18 µm in greatest width. Trapping nematodes by means of constricting rings.

Discussion: Cooke (1967 a) interpreted the conidial appendage as 'a result of precocious germination', but not as a taxonomically relevant feature at specific (Drechsler, 1952) or generic (Subramanian, 1963) level.

The length of the appendage is apparently variable (25-250 µm); a specific function of the appendage other than germination seems improbable. Furthermore, Cooke's observations that in many (older) cultures of *Monacrosporium* (e. g. *M. eudermatum*) aerial germ hyphae occur, have also frequently been confirmed in the course of this study.

Drechsler described his *Dactylella acrochaeta* later than his *D. doedycoides*, aware of the similarities. But even if the appendage is no more than a germ tube, differences between the two species remain:
-   the bases of conidia are convex rather than concave as in *M. doedycoides*;
-   the conidiophore tips are not regularly swollen as in *M. doedycoides*;
-   chlamydospores, but no conidial bodies (*M. doedycoides*) are produced. [p. 47]


Fig. 16
Drechsler's original illustration (iconotype) of *Monacrosporium acrochaetum* (Drechsler, 1952). Conidiophores, conidia with appendages, constricting rings, and trapped nematodes. (Reproduced by permission of the Mycological Society of America). [p. 48]


Fig. 17
Drechsler's original illustration (iconotype) of *Monacrosporium aphrobrochum* (Drechsler, 1950). Conidiophores, conidia, constricting rings, and trapped nematodes with assimilative hyphae inside. (Reproduced by permission of the Mycological Society of America). [p. 49]

2. Monacrosporium aphrobrochum (Drechsler) Subram. - Fig. 17.

Dactylella aphrobrocha Drechsler - Mycologia **42**: 20. 1950 • *Monacrosporium aphrobrochum* (Drechsler) Subram. - J. Indian bot. Soc. **42**: 293. 1963 • *Golovinia aphrobrocha* (Drechsler) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 140. 1979.
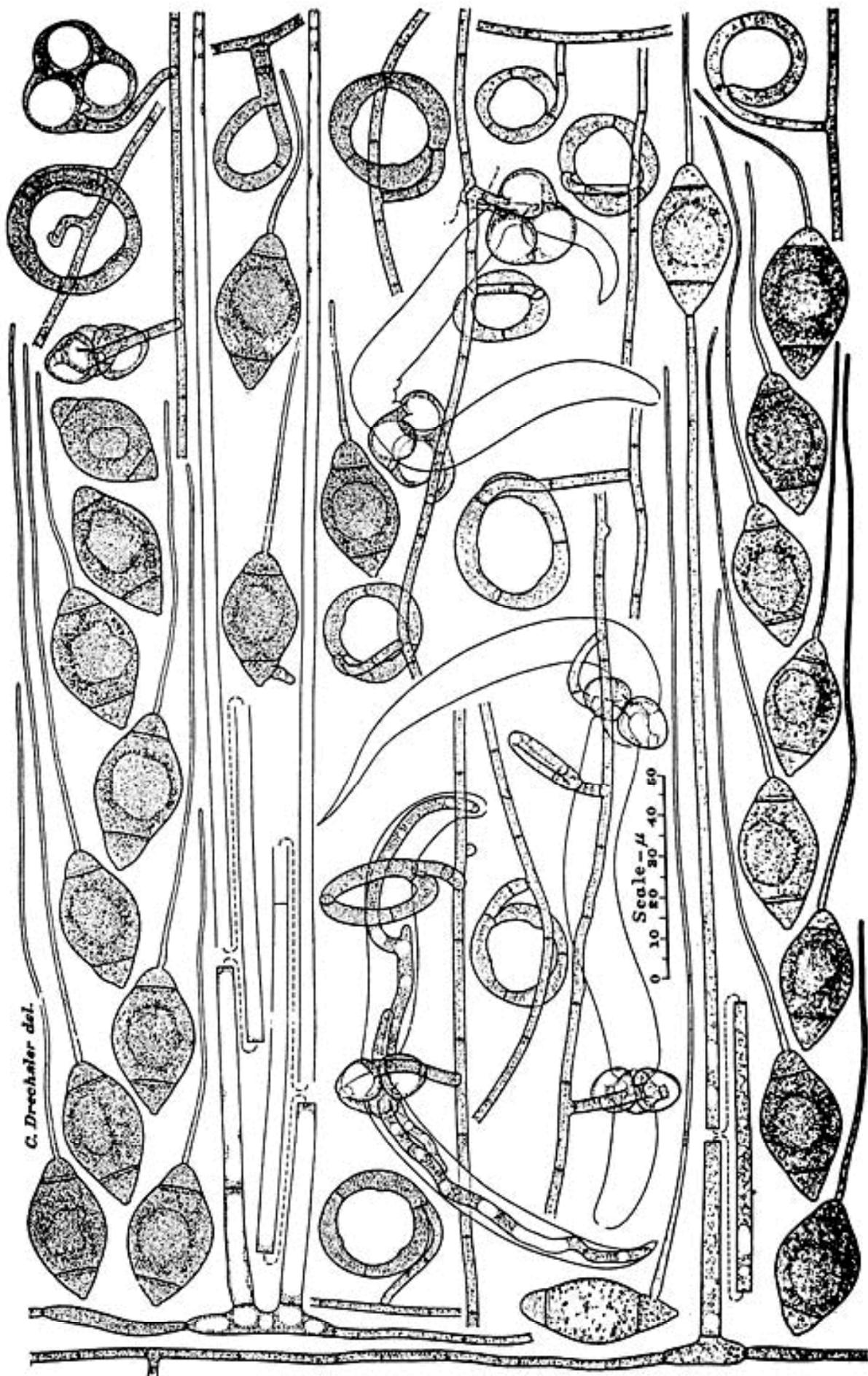
Fig. 16 Drechsler's original illustration (iconotype) of *Monacrosporium acrochaetum* (Drechsler, 1952). Conidiophores, conidia with appendages, constricting rings, and trapped nematodes. (Reproduced by permission of the Mycological Society of America). [p. 48]
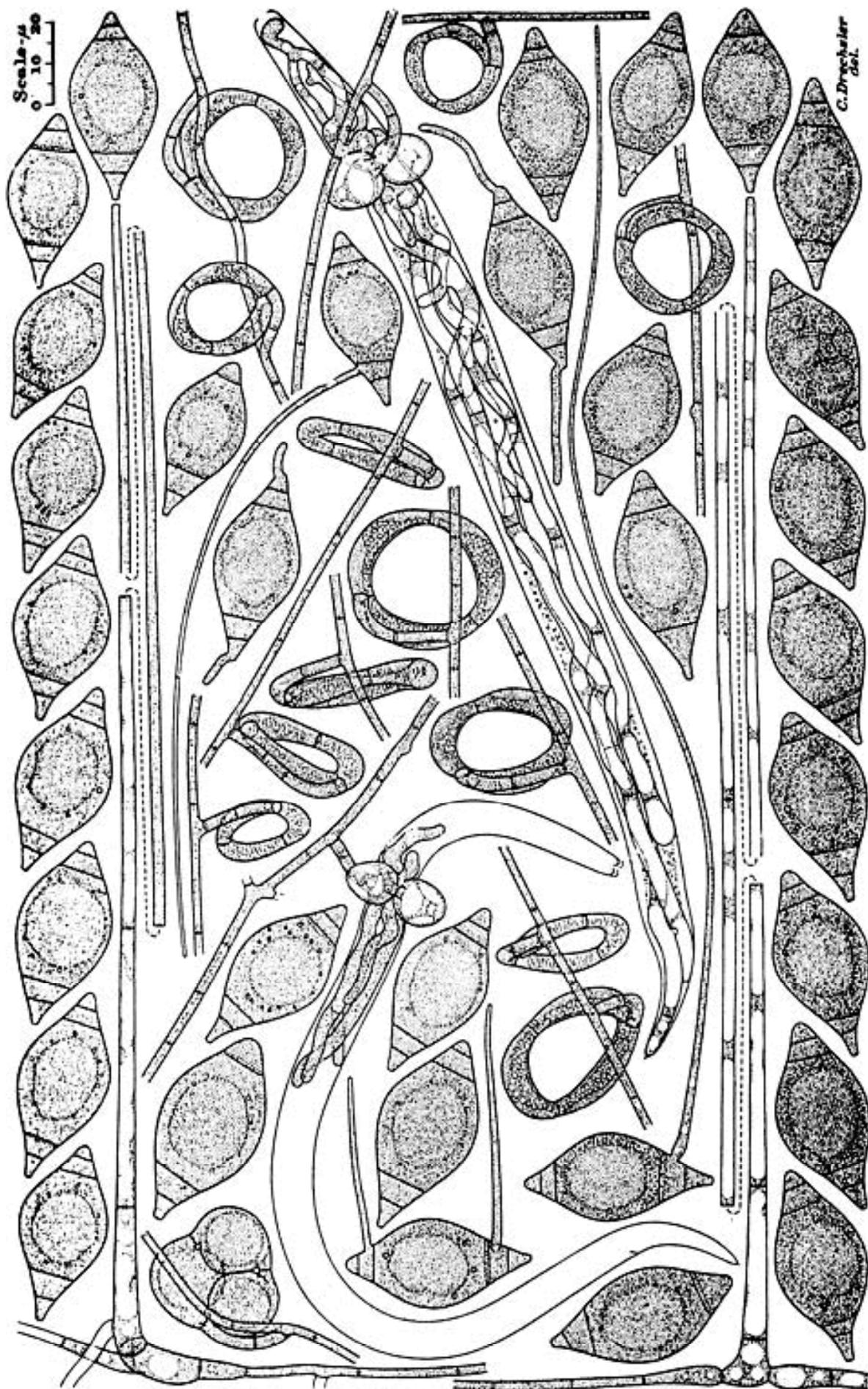
Fig. 17 Drechsler's original illustration (iconotype) of *Monacrosporium aphrobrochum* (Drechsler, 1950). Conidiophores, conidia, constricting rings, and trapped nematodes with assimilative hyphae inside. (Reproduced by permission of the Mycological Society of America). [p. 49]

Typification: Iconotype (Mycologia **42**: 14, 18).

Published descriptions: Soprunov (1958; p. 108).

Characteristics (after Drechsler, 1950)**:** Conidiophores usually 450-525 µm high, bearing a single conidium and sometimes a second one on a short perpendicular branch below the tip. Conidia (from nematode-infested agar) usually broadly spindle-shaped, most often divided by four cross-walls (in pure culture on cornmeal agar, however, mostly three-septate), 41-46.7-55 x 17-21.9-26 µm. Chlamydospores not observed. Trapping nematodes by means of constricting rings.

Discussion:
Conidial length and width of *M. aphrobrochum* is very similar to the older *M. coelobrochum* (Drechsler, 1947), but Drechsler (1950, l.c.) emphasized the greater conidial length and the protracted apical and basal cells of the latter.

3. Monacrosporium arcuatum (Scheuer & J. Webster) A. Rubner, *comb. nov.* - Fig. 18.

Basionym: *Dactylella arcuata* Scheuer & J. Webster - Mycol. Res. **94:** 718. 1990.

Typification: Holotype CBS H-4242; ex-type culture CBS 174.89 (= IMI 333702).

Characteristics:
Conidiophores bearing one conidium on the tip or 2-8 conidia on short branches (as in *M. haptotylum*); an additional cluster of conidia may be produced after proliferation of the conidiophore (Scheuer and Webster, 1990). Conidia fusiform, with a slightly rounded tip, widest below the middle, 30-45 x 4.5-6 µm, usually almost equidistantly three-septate, bearing a (sub-)globose adhesive knob (about 6.5 x 6 µm) on the tip (sometimes at both ends) at full maturity. Chlamydospores not observed. Trapping nematodes by means of adhesive knobs (about 10 x 7 µm), which may grow out to form branched or unbranched pluricellular structures.

Material examined:
CBS 174.89 (T), from decaying leaves of *Ammophila arenaria*, UK, 6 Dec. 1988.

Discussion:
Through the adhesive knobs on the conidia, a relation to *M. asthenopagum*, *M. leptosporum*, *M. lobatum*, and also to *Arthrobotrys haptospora* is given. *M. lobatum*, which shares a similar conidium morphology with *M. arcuatum*, has more clavate than fusiform and much wider conidia. The type of trapping organ formed on the hyphae, described by the original authors as 'multicellular arches, rings, networks by branching or anastomosis' neither fits in the category of sessile knobs nor of hyphal branches and three-dimensional networks. I found that the knobs only rarely proliferate (spontaneously on CMA:2 or induced by nematodes on WA), but when they do, they resemble the [p. 50] hyphal branches of *M. gephyropagum*. The elongated sticky cells produced on the hyphae differ in shape and size from the knobs occurring on the tip of the conidia.
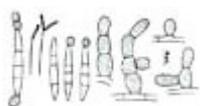

Fig. 18
Monacrosporium arcuatum, CBS 174.89 on CMA:2 (28 d) and on WA + nematodes (22 d). Habit sketch of conidiophores, conidia, partly with adhesive knobs; adhesive knobs formed on the hyphae.

4. Monacrosporium asthenopagum (Drechsler) A. Rubner, *comb. nov*. - Fig. 19

Basionym: *Dactylella asthenopaga* Drechsler - Mycologia **29**: 498. 1937 • *Dactylariopsis asthenopaga* (Drechsler) Mekht. - Mikol. Fitopatol. **1**: 279. 1967 (but returned to *Dactylella* by Mekhtieva in 1979).

Typification: Iconotype (Mycologia **29**: 497).

Published descriptions: Duddington (1951); Sachchidananda and Krishnan (1971); Kitz and Embree (1979); Fritsch and Lysek (1989).

Characteristics (after Drechsler, 1937)**:** Conidiophores (100-)125-175(-200) µm high, bearing only a single conidium, occasionally with one or two short broadly divergent branches below the tip. Conidia obconical or clavate, truncate at the narrow proximal end, broadly rounded at the distal end, 20-31.5-46 x 6.5-8.2-9.5 µm, typically three-septate. Chlamydospores not observed. Trapping nematodes by means of stalked knobs, which may also be formed on the conidia.

Material examined:
CBS 227.52 and 222.54 from decaying wood of *Quercus petraea* (CBS 227.52), UK, S.M. Dixon; not producing trapping organs and not sporulating.
CBS 262.83 (= IMI 143691), from soil, Queensland, Australia; not producing trapping organs, sporulating poorly, identity doubtful.
CBS 917.85, from decaying wood, Waterleidingsduinen, Vogelenzang, Netherlands, isol. [p. 51] W. Gams, det. G.S. de Hoog, Sept. 1985; sporulating abundantly, not producing trapping organs, resembling *Dactylella cylindrospora* (R.C. Cooke) A. Rubner. [p. 51]

Fig. 19
Drechsler's original illustration (iconotype) of *Monacrosporium asthenopagum* (Drechsler, 1937). Conidiophores, conidia, partly germinating with adhesive knobs, adhesive knobs formed on the hyphae, trapped nematodes (*Bunonema* spec.) with globose bodies and assimilative hyphae inside. (Reproduced by permission of the Mycological Society of America). [p. 52]

Discussion:
This is a rarely isolated species. Fritsch and Lysek (1989) reported it from soil over calcareous rocks; Duddington (1951) found it four times in the UK. The trapping organs resemble those of *M. ellipsosporum*.

   With its more or less clavate conidia, *M. asthenopagum* differs in conidial shape from most species of *Monacrosporium*. Therefore, according to the shape of conidia, it can be confused with non-predacious species, such as *Dactylella cylindrospora* (R.C. Cooke) A. Rubner or *Dactylella pulchra* (Linder) de Hoog & Oorschot.

5. Monacrosporium bembicodes (Drechsler) Subram. - Fig. 20.

Dactylella bembicodes Drechsler - Mycologia **29**: 491. 1937 • *Monacrosporium bembicodes* (Drechsler) Subram. - J. Indian bot. Soc. **42**: 293. 1963 • *Golovinia bembicodes* (Drechsler) Mekht. - Mikol. Fitopatol. **1**: 275. 1967.
= *Dactylella coprophila* Faurel & Schotter - Rev. Mycol. **30**: 157. 1965 [nom. inval., Art. 37 ICBN].
= *Dactylella megalobrocha* Glockling - Mycol. Res. **98**: 847. 1994.

Typification: Iconotype (Mycologia **29**: 489).

Published descriptions: Couch (1937 - trapping organs); Soprunov (1958; p. 108, 144); Matsushima (1975); Zachariah and Insell (1979 - trapping organs); Gray and Duff (1982).

Characteristics (after Drechsler, 1937)**:** Conidiophores (250-)300-450(-500) µm high, usually bearing a single conidium at the tip. Conidia (from nematode-infested cornmeal agar) top-shaped, broadly rounded at the apex, tapering toward the slightly protruding truncate base, 34-42-48 x 16-20-23 µm, regularly three-septate. Microconidia developing on conidiophores with several (3-7) subterminal denticles (2.5-4 µm long). Microconidia obovoid, 12-20 x 4.5-7 µm, usually one-septate, the septa being in the upper part (Drechsler, 1961, p. 21). Chlamydospores not observed. Trapping nematodes by means of constricting rings.

Material examined:
CBS 177.37, from nematode, isol./det./dep. C. Drechsler; not forming trapping organs and not sporulating. CBS 160.38, USA, J.N. Couch; forming stalked, three-celled rings, which do not constrict, poor sporulation.

Discussion:
A well-sporulating culture is lacking. Drechsler's iconotype shows conidia quite similar to many of the network-forming species, such as *M. psychrophilum* and *M. thaumasium.* Thus the trapping organ is a crucial distinctive feature. No living culture or dried material has been preserved of *Dactylella megalobrocha*, but the synonymy is evident from the description. [p. 53]

Fig. 20
Drechsler's original illustration (iconotype) of *Monacrosporium bembicodes* (Drechsler, 1937). Conidiophores, conidia, constricting rings, and trapped nematodes. (Reproduced by permission of the Mycological Society of America). [p. 54]

6. Monacrosporium coelobrochum (Drechsler) Subram. - Fig. 21.

Dactylella coelobrocha Drechsler - Mycologia **39**: 17. 1947 • *Monacrosporium coelobrochum* (Drechsler) Subram. - J. Indian bot. Soc. **42**: 293. 1963 • *Golovinia coelobrocha* (Drechsler) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 141. 1979.

Typification: Iconotype (Mycologia **39**: 7, 9).

Characteristics (after Drechsler, 1947)**:** Conidiophores 200-500 µm high, bearing a single conidium. Conidia mostly top-shaped and strongly ventricose in the middle, 46-53.7-64 x 18-21.2-25 µm, with 2-5 septa, but mostly inequidistantly four-septate. Chlamydospores not observed. Trapping nematodes by means of constricting rings.

Discussion:
For differences between *M. coelobrochum* and the similar *M. aphrobrochum* see p. 49.

7. Monacrosporium copepodii (G.L. Barron) A. Rubner, *comb. nov.* - Fig. 22.

Basionym: *Dactylella copepodii* - G.L. Barron - Can. J. Bot. **68**: 692. 1990.

Typification: Holotype Herbarium OAC 10847 (not seen), from composted manure, Auckland, New Zealand, Dec. 1988.

Characteristics (after Barron, 1990)**:** Conidiophores unbranched, 160-360 µm high, bearing a single conidium on the tip. Conidia (from Czapek's agar containing copepods) more or less fusiform, broadest in the middle, tapering to a narrow end, apically acutely rounded, 56-97 x 8.5-16 µm, one- to six-, mostly four-septate. Chlamydospores not observed. Capturing copepods by means of adhesive branches (100-180 µm long), sometimes with a distinct (sub-)globose apical cell (7.2-8.0 x 7.2-10 µm), otherwise terminal portion 5.4-6.8 µm wide. The globose cell or the terminal portion of the branch is covered with adhesive material.

Discussion:
Barron (1990) had no doubt about the new fungus being a member of the *Dactylella-Monacrosporium* complex. Conidia are fusiform, and when cultured on WA (without copepods) they are more uniform in size and shape than conidia from rich agar media. Conidia formed on WA (90-104 x 10.8-14.4 µm) closely resemble those of nematode-trapping fungi, such as *M. haptotylum*, though the latter species produces much smaller conidia. The morphology of the trapping organ differs somewhat from that described for nematophagous species of the genus.

   M. copepodii is, though capturing copepods and not nematodes, similar in many other aspects to other species of *Monacrosporium*: conidia may germinate with hyphal extensions which soon form an adhesive knob. Some conidia have a bifurcate apex, rendering them triradiate (compare *M. iridis*). [p. 55]

Fig. 21
Drechsler's original illustration (iconotype) of *Monacrosporium coelobrochum* (Drechsler, 1947). Conidiophores, conidia, and constricting rings. (Reproduced by permission of the Mycological Society of America). [p. 56]

Fig. 22
Monacrosporium copepodii, original illustration from Barron (1990). Conidiophore, conidia, partly with adhesive branches; adhesive branches with terminal globose knob formed on the hyphae.

8. Monacrosporium Doedycoides (Drechsler) R.C. Cooke & C.H. Dickinson - Fig. 23.

Dactylella doedycoides Drechsler - Mycologia **32**: 454. 1940 • *Monacrosporium doedycoides* (Drechsler) R.C. Cooke & C.H. Dickinson - Trans. Br. mycol. Soc. **68**: 622. 1965 • *Golovinia doedycoides* (Drechsler) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 136. 1979.

Typification: Iconotype (Mycologia **32**: 455).
Epitype: CBS 586.91 (= A.R. 901), dried culture preserved in herb. CBS.

Published descriptions: Muller (1958 - trapping organs); Soprunov (1958; p. 109); Lawton (1967 - trapping organs); Matsushima (1975); Zachariah (1982 - trapping organs); Gray (1983).

Characteristics: Conidiophores 250-400 µm high, sometimes branched in the middle part, with a knob-like tip (about 4 µm wide), bearing a single conidium. Conidia top-shaped, with a concavely truncate base, 32-40-50 x 14-19-23 µm, usually two-septate. Chlamydospores in chains. Trapping nematodes by means of constricting rings. [p. 57]

Fig. 23
Monacrosporium doedycoides; a. CBS 175.55 on CMA:2 (10 d). Habit sketch of conidiophores, conidiophore tips with swollen ends, and conidia; b. CBS 586.91 on CMA:2 (13 d, 90 d). Habit sketch of conidiophores, conidiophore tip with swollen end, conidia and chlamydospore chain.

Material examined:
CBS 233.54, A.J. Juniper, det. M. Peach, UK; forms stalked, three-celled rings, which do not constrict; not sporulating.
CBS 175.55, A.J. Juniper, det. S.M. Dixon, UK; forming stalked, three-celled rings, which do not constrict.
CBS 586.91 (= A.R. 901), from soil, forest of *Acacia*, Quinta de São Pedro, Portugal, coll./isol. A. Kaufhold, May 1990. [p. 58]

Discussion:
M. doedycoides seems to be well-defined by the following characters: (1) the knob-like tip of the conidiophore, (2) the concave conidium base, contrasting with 'a somewhat convexly rounded truncate outline usual in related forms' (Drechsler, l.c.), and (3) the 'conidioid bodies' described by Drechsler (l.c.) as arising on short branches (10-20 µm), being more or less cylindrical in shape and measuring 20-40 x 6-8 µm. The first and second characters could be observed in the two sporulating strains, the third was never found in any culture of any age. Instead, chlamydospores in chains (Fig. 23 b) were developed in a three-month-old culture (CMA:2 with oat chaff). A striking

difference between Drechsler's description and the two isolates CBS 175.55 and CBS 586.91 were the branched conidiophores (Fig. 23) and the conspicuously longer conidia of CBS 586.91: 37-47-64 µm. Both strains showed signs of degeneration: the apical conidial cell was frequently oblique. Sometimes even two oblique cells developed from the middle cell (CBS 175.55).

9. Monacrosporium drechsleri (Tarjan) R.C. Cooke & Dickinson - Fig. 24.

Dactylella drechsleri Tarjan - Mycopath. Mycol. appl. **14**: 143. 1961 • *Monacrosporium drechsleri* (Tarjan) R.C. Cooke & C.H. Dickinson - Trans. Br. mycol. Soc. **68**: 623. 1965 • *Golovinia drechsleri* (Tarjan) Mekht. - Mikol. Fitopatol. **1**: 276. 1967.

Typification: Holotype F1636 BPI (not seen).
Ex-type culture (probably): CBS 549.63, from soil of a citrus grove, Florida, USA.

Published descriptions: Heintz and Pramer (1972 - trapping organs).

Characteristics (after Tarjan, 1961)**:** Conidiophores mostly 145 µm high, often branched near the apex and bearing additional conidia on one or two short spurs. Conidia somewhat fusiform, with a finely truncate base, rounded at the distal end, 29.5-39.6-48.7 x 10.7-13.1-15.4 µm, predominantly three-septate. Chlamydospores not observed. Trapping nematodes by means of short-stalked knobs.

Material examined:
CBS 549.63 (T?), from soil of citrus grove, Florida, isol. A.C. Tarjan.
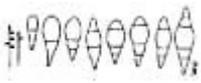

Fig. 24
Monacrosporium drechsleri, CBS 549.63 on CMA:2 (26 d) and CPA (60 d). Habit sketch of conidiophores, conidia. [p. 59]

Discussion:
CBS 549.63 shows somewhat smaller conidia (22-43.5 x 9.5-13 µm) than originally described, predominantly three-septate, but also four-septate. Conidiophores are much higher and produce more than two denticles (Fig. 24).

10. Monacrosporium effusum (Jarow.) Xing-Z. Liu & K.-Q. Zhang - Fig. 25.

Dactylaria effusa Jarow. - Bull. Acad. Pol. Sci. Cl. 5: Ser. Sci. biol. **16**: 773. 1968 • *Geniculifera effusa* (Jarow.) Oorschot - Studies in Mycology **26**: 93. 1985 • *Arthrobotrys effusa* (Jarow.) S. Schenck, W.B. Kendr. and Pramer - Can. J. Bot. **55**: 982. 1977 • *Monacrosporium effusum* (Jarow.) Xing-Z. Liu & K.-Q. Zhang - Mycol. Res. **98**: 864. 1994.
= *Arthrobotrys constringens* Dowsett, J. Reid & Kalkat - Mycologia **76**: 559. 1984.

Typification: Iconotype (Bull. Acad. Pol. Sci. Cl. 5: Ser. Sci. biol. **16**: 775, Figs 1-28).
Epitype: CBS 774.84, type culture of *A. constringens*, dried culture in CBS.

Published descriptions: Van Oorschot (1985).

Characteristics (after Jarowaja, 1968)**:** Conidiophores simple, 270-350 µm high, bearing first a single conidium, later additional conidia on denticles or longer geniculate branches. Conidia ellipsoid, 30-40-50 x 17-21-26 µm, mostly inequidistantly two-septate. Microconidiophores present in older cultures, geniculate. Microconidia clavate, 18-26 x 9-10.5 µm, non-septate or with one septum in the middle or somewhat above. Chlamydospores not observed. Trapping nematodes by means of constricting rings.

Material examined:
CBS 774.84 (type culture of *A. constringens*), from marsh soil, University Field Station, Delta Marsh, Manitoba, Canada, isol./det. J. Reid.

Discussion:
CBS 774.84 formed conidia very variable in shape, size and septation (Fig. 25), but did not suggest a differentiation in macro- and microconidia as observed by Jarowaja (1968). Dowsett *et al.* (1984) distinguished primary and secondary conidia, which were 37.5-45 x 22-30 µm (three-celled) and 21.5-35 x 10-15 (two-celled), respectively. The material examined (CBS 774.84) comes closer to the latter than to the original description of *D. effusa*, although a line between the two conidial forms could not always be drawn. Conidiophores (on CMA:2 and PCA) only bore one conidium or an additional conidium on a geniculate branch. (After induction with nematodes rings were formed, which did not constrict and capture nematodes.)
    The two species were already regarded as synonymous by Van Oorschot (1985). Because of the differences between my observations on CBS 774.84 and the original description of *A. constringens*, as well as differences between the original descriptions for *G. effusa* and *A. constringens*, a considerable variation in conidial characters must be admitted for this species. The geniculate conidiophore and the often two-septate conidia place it in *Monacrosporium*. [p. 60]
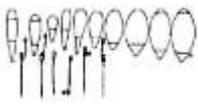
Fig. 25
Monacrosporium effusum, CBS 774.84, partly on CMA:2 (60 d), partly CPA (21 d). Habit sketch of conidiophores, macro- and microconidia.

11. Monacrosporium elegans Oudem. - Fig. 26.

Monacrosporium elegans Oudem. - Ned. kruidk. Archf., Ser.2, 4: 250. 1885 • Golovinia elegans (Oudem.) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 142. 1979.

Typification: Holotype in L. Epitype: CBS 301.94 (= A.R. 9338), dried culture preserved in CBS.

Published descriptions: Marchal (1895); Rostrup (1916).

Characteristics: Conidiophores 150-265-400 µm high, bearing a single conidium on the tip or some additional conidia on small perpendicular and sometimes longer, geniculate branches. Conidia top-shaped, 40-52-65 x 17-20-23 µm, commonly three-septate, the inequidistantly distributed septa demarcating a small apical cell, a strongly ventricose and large middle cell, a parabasal and a basal cell. Microconidia obovoid, protracted at the base, 13-16.5 x 5-6 µm, nonseptate. Chlamydospores not observed. Trapping nematodes by means of three-dimensional networks.

Material examined:
L 9096 (T), from rabbit dung, Amsterdam, The Netherlands, C.A.J. Oudemans, 1883; permanent slide.
CBS 299.94 (= A.R. 9229), from soil of a laurel forest, Las Mercedes, Tenerife, coll./isol. G. Lysek, 1989.
CBS 300.94 (= A.R. 9232), from moss cushion, Berlin-Dahlem, coll./isol. S. Behnke, 1992.

Fig. 26a
Monacrosporium elegans, original illustration from Oudemans (1885). Conidiophore with conidium. [p. 61]
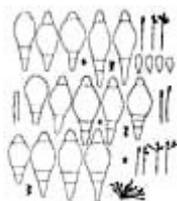
Fig. 26 b-d
Monacrosporium elegans; b. CBS 397.93 on CMA:2 (11 d, 50 d). Habit sketch of conidiophores, macro- and microconidia; c. CBS 301.94 on CMA:2 (10 d). Habit sketch of conidiophores, conidiophore tip, and macroconidia; d. CBS 300.94 on CMA:2 (15 d, 60 d). Habit sketch of conidiophores, formed singly and in clusters; macroconidia. [p. 62]

CBS 316.94 (= A.R. 937), from soil, Olmedo, Ecuador, 13 March 1993.
CBS 301.94 (= A.R. 9338), from dung of sheep, Lebus (Brandenburg), Germany, 10 Oct. 1993 (epitype).
L.P. 901, L.P. 906, CBS 397.93 (= L.P. 9011), L.P. 9022, L.P. 9030; from agricultural fields (L.P. 901, L.P. 906), pasture (L.P. 9011, L.P. 9022), and rhizosphere of wheat (L.P. 9030), Sweden, 9 May 1989 and 10 Aug. 1990, respectively, coll./isol. L. Persmark.

Discussion:
As stated on p. 4, *M. elegans* is the lectotype species of the genus. The material studied here matches the meagre original description and the type slide. Oudemans indicated conidia measuring 50-60 x 16-21 µm and a conidiophore of 250 µm length. The type material, a permanent slide, confirms the conidial length and approximately the conidial width. The average width of ten conidia was found to be 22.5 µm, larger than indicated by Oudemans. (It is possible that through preparation conidia have become flattened and broadened.) The length could be measured only in four conidia in the permanent slide, as the basal and parabasal cells were collapsed or hidden by the original substrate. Conidiophores could not be found in the microscopical slide.

Table 5: Comparison of species similar to *M. elegans* (published data) and strains of *M. elegans* and *M. psychrophilum* (own measurements).

Strain	conidioph. length and tip		conidia	trap
M. elegans (after Oudem.)	250	simple	50-60 x 16-21	?
CBS 301.94 (epitype)	200-400	simple	43-54-61 x 16-20-22	network
CBS 316.94 (*M. elegans*)	?	side branches?	46-50.5-62 x 17-21.5-22	network
CBS 299.94 (*M. elegans*)	250-360	side branches	35-46.5-54 x 17-21-23	network

CBS 300.94 (*M. elegans*)	150-310	side branches	40-52.5-61 x 17-19.5-21	network
L.P. 9022 (*M. elegans*)	?	simple	38-55.5-68 x 17-20-22	network
M. psychrophilum	150-500	denticles, partly geniculate	46-71 x 21-29	network
CBS 318.94 (*M. psychroph.*)	150-400	simple	44-48-54 x 17-20-23	network
CBS 319.94 (*M. psychroph.*)	250-300	simple	46-52-60 x 18-21-23	network
M. bembicodes	200-450	simple	34-48 x 16-23	constr.rings
M. eudermatum	400-500	denticles, partly geniculate	37-55 x 21-35	
M. megalosporum	350-450	denticles	40-75 x 18-35	network
M. robustum	150-450	simple	68-85 x 20-30	branches
M. thaumasium	250-450	denticles	27-46 x 15-23	network

The only reports of *M. elegans* after its publication are from Marchal (1895) and Rostrup (1916). However, these authors did not elucidate the species. Marchal thought [p. 63] of a variety of *M. elegans* because the conidia of his fungus only measured 20-40 x 15-18 µm. Rostrup's fungus is illustrated as having four-septate and ellipsoid conidia, strongly suggesting *M. ellipsosporum*.

M. elegans has not been reported since 1935 (Rostrup, without details), and no further adequate description or drawing exists. Hence it is possible that some later described species turns out to be a synonym.

Drechsler always was aware of *Monacrosporium* (and typification). He tried to find *M. elegans* in many of his isolates, but he then introduced them under other names, listing the differences from *M. elegans*. For his *Dactylella bembicodes* he found a general resemblance of the conidia to those of *M. elegans*, but they differed in detail (length of conidiophores and conidia). *Dactylaria gephyropaga*, *Dactylaria thaumasia* and *Dactylaria psychrophila*, also resemble *M. elegans*, but differ in conidial sizes and the vegetative stage, respectively (Drechsler, 1937). Drechsler already regarded *M. elegans* as most probably being a member of the predacious series, because of its ventricose conidia which are infrequent in other fungal groups.

The probability of *M. elegans* being a nematode-trapping fungus is very high indeed. The fungus was originally described from rabbit dung, a substratum rich in nematophagous fungi (e. g. Juniper, 1954). In Table 5 the characters of *M. elegans* given by Oudemans are compared with other similar species (measurements taken from the original descriptions) and with strains of *M.* cf. *psychrophilum*, which are closest to *M. elegans*.

The average conidial measurements of the epitype culture CBS 301.94 are 54 x 20 µm (n = 60; s.d. = 4.4 and 1.6 µm, respectively).

CBS 318.94 and 319.94 were identified as *M. psychrophilum* (Rubner, 1994, and p. 92-93), though they are morphologically intermediate and close to *M. elegans*. CBS 300.94 also resembles *M. psychrophilum* (mainly in the shape and measurements of conidia - Fig. 26 d), but it was decided to leave it in *M. elegans*. This isolate seems to illustrate the widest range of variation in *M. elegans*: the conidiophores are strongly geniculate, and in an older culture cushions of short conidiophores are developed (Fig. 26 d).

12. Monacrosporium ellipsosporum (Preuss) R.C. Cooke & C.H. Dickinson - Fig. 27.

Menispora ellipsospora Preuss in Sturm - Deutschl. Fl. Abt. 3: H.8: T.47. 1851 • *Dactylella ellipsospora* (Preuss) Grove - J. Bot. Lond. **24**: 200. 1886 • *Monacrosporium ellipsosporum* (Preuss) R.C. Cooke & C.H. Dickinson [as '(Grove) R.C. Cooke & C.H. Dickinson'] - Trans. Br. mycol. Soc. **48**: 623. 1965 • *Dactylaria ellipsospora* (Preuss) Zachariah - Can J. Microbiol. **29**: 1295. 1983 [nom. inval., Art. 33 ICBN] • *Golovinia ellipsospora* (Preuss) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 144. 1979 [nom. inval., Art. 33 ICBN].
? = *Monacrosporium leporinum* Bubák, Annls mycol. 4: 120. 1906. [p. 64]
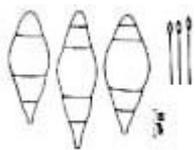
Fig. 27
Monacrosporium ellipsosporum, CBS 302.94 on CMA:2 (17 d). Habit sketch of conidiophores and conidia.

Typification: Authentic material of *Menispora ellipsospora* is not preserved in B and could not be found in Klotzsch Herbarium vivum mycol. (in B).
Neotype: CBS 302.94 (= A.R. 931), dried culture preserved in CBS.

Published descriptions: Drechsler (1937); Duddington (1950); Faust and Pramer (1964); Matsushima (1971, 1975); Gray (1983); Zachariah (1983 b - trapping organs).

Characteristics:

Conidiophores 150-270 µm high, bearing a solitary conidium. Conidia broadly spindle-shaped, rounded on the tip, 40-44-50 x 12-15-16 µm, commonly four-septate. Chlamydospores not observed. Trapping nematodes by means of stalked knobs.

Material examined:
CBS 224.54, isol. A.J. Juniper, det. S.M. Dixon, UK; does not sporulate.
CBS 225.54, isol. A.J. Juniper, det. M. Peach, UK; conidial sizes suggest *M. lysipagum*.
A.R. 9131 and 9133, from soil in warm greenhouse, Botanic Garden, Berlin-Dahlem, 30 Aug. 1991 and 30 Aug. 1993.
A.R. 9143, from soil in cold greenhouse, Botanic Garden, Berlin-Dahlem, 30 Aug. 1991.
A.R. 926, from soil in warm greenhouse, Botanic Garden, Berlin.-Dahlem, 17 March 1992.
A.R. 929, from rhizosphere of orchids in warm greenhouse, Botanic Garden, Berlin-Dahlem, 17 March 1992.
CBS 303.94 (= A.R. 9212), from dead wood, Kronwald near Loitz, Mecklenburg, Germany, 18 May 1992.
CBS 302.94 (= A.R. 931), from soil of a pine forest, Virgen del Pino, Tenerife, Oct. 1992, coll. G. Lysek.
CBS 394.94 (= A.R. 9332), from leaf litter of *Larix decidua*, Botanic Garden, Berlin-Dahlem, 22 Aug. 1993.

Discussion:
The identity of Preuss' fungus would be very doubtful if Grove had not given a better description. It is in this sense that the species was taken up by subsequent [p. 65] authors and is neotypified here. Conidia vary strongly in size, as already observed by Drechsler (1937).

13. Monacrosporium eudermatum (Drechsler) Subram. - Fig. 28.

Dactylaria eudermata Drechsler - Mycologia **42**: 40. 1950 • *Monacrosporium eudermatum* (Drechsler) Subram. - J. Indian bot. Soc. **42**: 293. 1963• *Genicularia eudermata* (Drechsler) Rifai - Reinwardtia **7**: 367. 1968 • *Geniculifera eudermata* (Drechsler) Rifai - Mycotaxon **2**: 216. 1975 • *Golovinia eudermata* (Drechsler) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 153. 1979.
= *Monacrosporium rutgeriense* R.C. Cooke & Pramer [as '*rutgeriensis*'] - Phytopathology 58: 544. 1968 [nom. inval., Art. 37 ICBN].

Fig. 28
Monacrosporium eudermatum; a. CBS 305.94 on CMA:2 (10 d, 26 d). Macroconidiophore tips, terminally branched; macroconidia, microconidiophores and microconidia; b. A.R. 9315 on CMA:2 (14 d; 75 d). Conidiophore tips, terminally branched; macroconidia, and chlamydospore chain. [p. 66]

Typification: Iconotype (Mycologia **42**: 32, 43, 38).
Epitype: CBS 305.94 (= A.R. 9321), dried culture preserved in CBS.

Published descriptions: Soprunov (1958; p. 105); Rifai (1968); Sachchidananda and Krishnan (1971).

Characteristics:
Conidiophores 230-370 µm high, bearing a single conidium or 1-3 additional conidia on short, geniculate branches. Conidia almost globose or broadly turbinate, 31-42-40 x 19-25-28.5 µm, mostly inequidistantly three-septate. Microconidia ellipsoid, 15-20 x 6-7 µm, nonseptate. Chlamydospores present in older cultures, forming chains or clusters, smooth-walled. Trapping nematodes by means of three-dimensional networks.

Material examined:
CBS 769.85 (received as *M. rutgeriense*), W.D. Rosenzweig (no indication of origin, not even in Rosenzweig, 1984).
CBS 584.91 (= A.R. 918), from soil in warm greenhouse, Botanic Garden, Berlin-Dahlem, 4 Feb. 1991.
A.R. 9132, from soil in warm greenhouse, Botanic Garden, Berlin-Dahlem, 4 Feb. 1991.
A.R. 925, from composted soil, Berlin-Dahlem, coll./isol. G. Saxena; resembles *M. thaumasium*.
A.R. 9228, from soil, roadside, Buenavista, Tenerife, coll./isol. G. Lysek, 1989.
A.R. 9315, from dry soil, Machalilla National Park, Ecuador, 11 March 1993.
A.R. 9317 from soil, Machalilla National Park, Ecuador, 11 March 1993.
CBS 305.94 (= A.R. 9321), from soil, La Palma, Oct. 1992, coll. G. Lysek, isol. M.Gödecke.

Discussion:
The delimitation of *M. eudermatum* against *M. psychrophilum* and *M. thaumasium* is not quite clear. According to Drechsler (1950), conidia of *M. eudermatum* are considerably wider than in *M. thaumasium*, and chlamydospores are lacking. As mentioned above (Chapter 4.4, p. 13), the presence or absence of chlamydospores is not a reliable criterion, thus conidial width must be the decisive character of *M. eudermatum*. No strain of the network-forming *Monacrosporium* species could be found with an average width of 28 µm, as originally indicated for *M. eudermatum*, but average conidial widths exceeding 23 µm or 19.2 µm (*M. thaumasium*) were often observed, see Table 6. In addition, these strains tended to produce geniculate conidiophores, carrying up to four conidia per conidiophore; they produced broad and irregularly three-septate conidia. Drechsler (1950) reported conidial sizes and septation from a pure culture differing from those observed in a nematode-infested culture, and interpreted this fact as 'pathological abnormalities deriving from nutritional deficiency'. This observation seems to be a characteristic feature of this species and has often given a hint for identification. In Table 6 eight strains are listed, together with their characteristics in the conidial apparatus.

CBS 305.94 and A.R. 9315 fit Drechsler's description of *M. eudermatum* best. The former produces microconidia and chlamydospores in old cultures. A.R. 9315 also shows a few chlamydospores in chains in an

80-day-old culture. A.R. 9317 produces [p. 67] very small conidia and does not fit the species concept well; however, it does not fit any other species better (Rubner, 1994).

Table 6: Comparison of several strains assigned to *M. eudermatum*.

strain	conidial measurements (in µm)	length : width	no. of conidia
CBS 984.91	35-44-52 x 18.5-25.5-28.5	1.73	4
A.R. 9132	35.5-39-43.5 x 18.5-21.5-24	1.81	?
A.R. 925	38.5-46.5-51 x 20.5-22.5-24	2.07	2
A.R. 9228	36-42.5-45.5 x 22-23-24	1.83	1
A.R. 9315	36.5-42-48 x 22-26.5-28.5	1.85	3
A.R. 9317	31-34.5-38 x 16-20.5-23.5	1.68	2
A.R. 9321	31-38-42.5 x 21-23.5-25	1.64	3
CBS 769.85	31.5-37.5-44.5 x 19-22-25.5	1.70	1

M. rutgeriense is regarded as a synonym of *M. thaumasium*. The isolate of Rosenzweig (CBS 769.85), which perfectly fits the description of *M. rutgeriense*, does not differ from the isolates named *M. eudermatum*. Cooke and Pramer (1968) were aware of such difficulties in *Monacrosporium*. They stressed the paucity of characters and the 'pronounced polymorphism' of some species.

14. Monacrosporium fusiforme R.C. Cooke & C.H. Dickinson - Fig. 29.

Monacrosporium fusiforme R.C. Cooke & C.H. Dickinson [as '*fusiformis*'] - Trans. Br. mycol. Soc. **48**: 628. 1965 • *Golovinia fusiformis* (R.C. Cooke & C.H. Dickinson) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 160. 1979.

Typification: Holotype IMI 109553 (apparently lost).

Characteristics (after Cooke and Dickinson, 1965)**:** Conidiophores simple, bearing a single conidium; sometimes a second conidium is formed on an about 15 µm branch near the conidiophore apex. Conidia fusiform to fusiform-ellipsoidal, 42.5-62.5 x 12.5-17.5 µm, mainly two- and three-septate. Chlamydospores not observed. Trapping nematodes by means of three-dimensional networks.
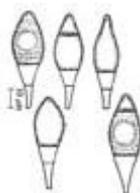
Fig. 29
Monacrosporium fusiforme, original illustration from Cooke & Dickinson (1965). Conidia. (Reproduced by permission of the British Mycological Society).

Discussion:
Cooke and Dickinson (1965) mentioned similarities to *M. psychrophilum* and to *M. salinum.* But the shape, dimensions, and septation of conidia made the new [p. 68] species distinct. In the absence of living or dead material it is difficult to decide how close *M. fusiforme* is to other network-forming species of *Monacrosporium*.

15. Monacrosporium gampsosporum (Drechsler) A. Rubner, *comb. nov.* - Fig. 30.

Basionym: *Dactylaria gampsospora* Drechsler - Sydowia **15**: 9. 1962 ('1961') • *Arthrobotrys gampsospora* (Drechsler) S. Schenck, W.B. Kendr. & Pramer - Can. J. Bot. **55**: 982. 1977 • *Dactylella gampsospora* (Drechsler) de Hoog & Oorschot - Stud. Mycol. **26**: 110. 1985 • *Woroninula gampsospora* (Drechsler) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 112. 1979.
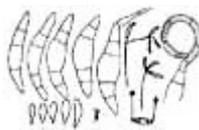
Fig. 30
Monacrosporium gampsosporum, CBS 512.61 on WA+N (20 d). Habit sketches of macroconidiophores and of microconidiophores germinating from a macroconidium; macro- and microconidia, adhesive loop developed by the basal cell of a macroconidium.

Typification: Holotype in BPI, No. 71640 (not seen). Ex-type culture: CBS 512.61 (= ATCC 14446).

Characteristics (after Drechsler, 1962)**:** Primary conidiophores mostly 150-625 µm high, with 2-7 short branches or spurs on the tip, on which conidia are borne forming a loose head. Primary conidia spindle-shaped, sometimes

curved, 25-76 (mostly 40-70) x 7-16 (mostly 9-14) µm, most often four-septate. Secondary conidiophores arising [p. 69] from detached conidia or from vegetative hyphae, 75-125 µm high, on the tip with short spurs (1.2-2 µm long), each bearing a conidium. Secondary conidia elongate obovoid, mostly 10-17 x 4-6 µm, nonseptate. Chlamydospores barrel-shaped or globose, mostly 8-21 x 6-17 µm, often produced abundantly in chains or aggregated in sclerotium-like masses. Trapping nematodes by means of three-dimensional networks.

Material examined:
CBS 512.61, from friable leaf mould, near Lake Alfred, Florida, USA, isol./det. C. Drechsler, 16 Apr. 1959.

Discussion:
The species seems to be well-delimited by its long, fusiform and frequently curved conidia. The branches of the conidiophore, 'tooth-like projections' (Drechsler, 1962) are somewhat longer than indicated by the author. The species is better accommodated in *Monacrosporium* than in *Arthrobotrys*, because the conidiophore is not arthrobotroid and because of the large, multiseptate conidia, often inflated in the middle.

16. Monacrosporium gephyropagum (Drechsler) Subram. - Fig. 31.

Dactylella gephyropaga Drechsler - Mycologia **29**: 512. 1937 • *Monacrosporium gephyropagum*(Drechsler) Subram. - J. Indian bot. Soc. **42**: 293. 1963 • *Golovinia gephyropaga* (Drechsler) Mekht. - Mikol. Fitopatol. **1**: 276. 1967.
= *Dactylella cionopaga* Drechsler - Mycologia **42**: 30. 1950 • *Monacrosporium cionopagum* (Drechsler) Subram. - J. Indian bot. Soc. **42**: 293. 1963 • *Golovinia cionopaga* (Drechsler) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 166. 1979.

Typification: Iconotype (Mycologia **29**: 511).
Ex-type culture: CBS 228.37, dried culture preserved in CBS.
M. cionopagum: Iconotype (Mycologia **42**: 25, 27).

Published descriptions: Duddington (1950); Soprunov (1958; p. 107); Das Gupta *et al.* (1964); Cooke and Cooke (1969); Tzean and Estey (1979 - trapping organs); El Amin (1980); Gamundí and Spinedi (1982); Gray and Duff (1982); Dowsett *et al.* (1984 - trapping organs); Mouchacca (1987); Fritsch and Lysek (1989, 1992).

Characteristics:
Conidiophores mostly simple, sometimes (depending on the isolate) with one lateral branch below the tip and rarely geniculate or even branched near the tip. Macroconidia spindle-shaped, 40-49-60 x 16-19.5-23.5 µm, mostly four-septate. Microconidia elongate ellipsoid, 18.5-24-27.5 x 5-6.6-8.5 µm, one-septate. Chlamydospores not observed. Trapping nematodes by means of adhesive hyphal branches, which have the tendency to fuse to a scalariform (two-dimensional) network.

Material examined:
CBS 178.37 (T of *M. gephyropagum*), ex nematode, USA, C. Drechsler; producing microconidia and sticky hyphal outgrowths.
CBS 228.52 (received as *D. cionopaga*), ex nematode, UK, C.L. Duddington; not sporulating, but still producing sticky hyphal outgrowths.
CBS 229.52, from decaying leaf, Surrey, Effingham, UK, M. Peach (received as *D. heptameres*, but reidentified here). [p. 70]
CBS 846.70, from litter, Meathop Wood, Westmorland, UK, isol. J.C. Frankland (No. M 7315), received as *M. bembicodes*, reidentified here as *M. gephyropagum* (because of adhesive hyphal branches).
CBS 197.73, from decaying wood, Germany, W. Gams.
A.R. 904, from coniferous leaf litter, Berlin, 12 March 1990.
A.R. 9022, from soil, New Mexico, USA, coll. M. Rubner, Aug. 1990.
A.R. 9116, 9123, 9129, 9140, 9219, 9220, from soil in warm greenhouse, Botanic Garden, Berlin-Dahlem.
A.R. 9138, from soil in cold greenhouse, Botanic Garden, Berlin-Dahlem, 30 Aug. 1991.
A.R. 9217, from composted soil, Berlin, 28 Apr. 1992.
A.R. 9218, from soil, Spain, coll. C. Oberprieler, 10 July 1992.
A.R. 9224, from soil, Battaglia, Italy, 1989, coll. G. Lysek, isol. M.Gödecke.
CBS 308.94 (= A.R. 9225), from soil, Montaña Ayara, Tenerife, 1989, coll. G. Lysek, isol. M. Gödecke.
A.R. 9227, from soil, Buenavista, Tenerife, 1989, coll. G. Lysek, isol. M.Gödecke.
CBS 309.94 (= A.R. 9230), from agricultural soil, Battaglia, Italy, 1989, coll. G. Lysek, isol. M.Gödecke.
A.R. 9231, substrate unknown, Berlin, 1992, coll./isol. G. Saxena.
CBS 310.94 (= A.R. 9234), from moss cushion, Berlin, 1992, coll./isol. S. Behnke.
CBS 398.93 (= L.P. 9020), L.P. 9023, L.P. 9024, L.P. 9025, L.P. 9032 from soil of agricultural fields, Sweden, May 1989 and Oct. 1990 respectively, coll./isol. L. Persmark.
A.R. 9319, from soil, La Palma, Spain, coll. G. Lysek, isol. M.Gödecke, Oct. 1992.
CBS 311.94 (= A.R. 9328), from leaf litter, Botanic Garden, Berlin-Dahlem, 22 Aug. 1993.

Discussion:
Among the species of *Arthrobotrys* and *Monacrosporium*, only *M. cionopagum* and *M. gephyropagum* form adhesive hyphal branches. Drechsler distinguished *M. cionopagum* from *M. gephyropagum* by simple adhesive branches, which seldom link to a scalariform network, while they commonly fuse in the latter. Conidiophores were found to be generally shorter, conidia noticeably longer (up to 60 µm) in *M. cionopagum* than in *M. gephyropagum*. Conidia of *M. cionopagum* show a conspicuous vacuole and vary in their septation more than in *M. gephyropagum*. From the sites of isolation and their behaviour in laboratory cultures Drechsler suggested that *M. cionopagum* was better adapted to cool climates than *M. gephyropagum*.

   I could not draw a line among the many isolates with adhesive (scalariform) branches studied. No isolate exactly matched the specific criteria given by Drechsler for one or the other species. However, the observations of almost

20 strains revealed features not described previously for one or the other taxon:
- conidiophores carrying one or more conidia: A.R. 9217 and L.P. 9025 with denticles similar to *M. thaumasium*, CBS 311.94 with branched and geniculate conidiophores (Fig. 31 d).
- some isolates producing only three-septate conidia: CBS 311.94 and L.P. 9023.
- adhesive branches fusing to form more complex structures than the ladder-shaped type: CBS 310.94.
- isolates with the *gephyropagum*-type trapping organs often originating from soils of warmer regions as observed by Drechsler (1937). These isolates, however, do not necessarily correlate in their reproductive structures with the *gephyropagum*-type. [p. 71]

Fig. 31
Monacrosporium gephyropagum; a. A.R. 9217 on CMA:2 (9 d, 16 d). Conidiophore tips, partly geniculate; macroconidia; b. CBS 310.94 on CMA:2 (8 d, 16 d). Anastomosing adhesive branches; c. A.R. 9319 on CMA:2 (10 d, 19 d). Habit sketch of microconidiophores, macro- and microconidia; d. CBS 311.94 on CMA:2 (40 d) and WA+N (48 d). Habit sketch of conidiophores and macroconidia; e. L.P. 9025 on CMA:2 (9 d, 51 d). Habit sketch of conidiophores and macroconidia, partly with adhesive knobs [p. 72].

Fig. 31 shows a selection of six isolates (CBS 308.94, 310.94, 311.94, A.R. 9217, 9319, L.P. 9025) demonstrating the variability of *M. gephyropagum* concerning the appearance of conidiophores, conidial shape, microconidia and trapping organs. Table 7 lists the conidial measurements of ten isolates, which were studied intensively.

Cooke and Cooke (1969) analysed five strains with lateral adhesive branches and noted that "the five isolates tend to bridge the gap between the two described 'species' and are not always separable on all three available criteria". The authors proposed to consider the strains as either a single species or as an at present unresolvable species complex. This view is supported by the present observations.

Table 7: Conidial measurements of isolates of *M. gephyropagum* (length and width), including the average for 25 or more conidia and standard deviations (s.d.).

A.R. 9217	38-43 (s.d. 3.4)-50.5 x 15-17.5 (s.d. 2.1)-23.5 µm
A.R. 9218	40-45.5 (s.d. 3.7)-52 x 17.5-20 (s.d. 1.1)-22 µm
CBS 308.94	46-50 (s.d. 2.5)-55 x 17.5-18.5 (s.d. 0.8)-19 µm
A.R. 9227	42.5-48 (s.d. 2.3)-53.5 x 19.5-22 (s.d. 1)-24 µm
CBS 309.94	44-49.5 (s.d. 3.8)-57 x 16-18 (s.d. 1.7)-20 µm
CBS 310.94	47.5-52 (s.d. 3.6)-61.5 x 16-18.5 (s.d. 1.2)-20 µm
A.R. 9319	42.5-48.5 (s.d. 2.3)-52 x 17.5-21 (s.d. 1.4)-22 µm
A.R. 9328	41-46 (s.d. 2.7)-55 x 19-20.5 (s.d. 1)-22.5 µm
CBS 311.94	42.5-48 (s.d. 5.2)-60 x 13.5-15.5 (s.d. 1.6)-19 µm
L.P. 9025	44-48.5 (s.d. 3.4)-55 x 16-19 (s.d. 1.3)-21.5 µm

17. Monacrosporium haptotylum (Drechsler) Xing-Z. Liu & K.-Q. Zhang **-** Fig. 32.

Dactylaria haptotyla Drechsler - Mycologia **42**: 48. 1950 • *Golovinia haptotyla* (Drechsler) Mekht. - Mikol. Fitopatol. **1**: 277. 1967 • *Candelabrella haptotyla* (Drechsler) Rifai - Reinwardtia **7**: 369. 1968 • *Arthrobotrys haptotyla* (Drechsler) S. Schenck, W.B. Kendr. & Pramer - Can. J. Bot. **55**: 983. 1977 • *Dactylella haptotyla* (Drechsler) de Hoog & Oorschot - Stud. Mycol. **26**: 111. 1985 • *Monacrosporium haptotylum* (Drechsler) Xing-Z. Liu & K.-Q. Zhang - Mycol. Res. **98**: 865. 1994.

? = *Dactylium candidum* Nees - Syst. Pilze Schw. **58**. 1817: Fries Syst. mycol. **3**: 44. 1829 • *Dactylaria candida* (Nees : Fr.) Sacc. - Syll. Fung. **4**: 195. 1886 • *Candelabrella candida* (Nees : Fr.) Rifai - Reinwardtia **7**: 369. 1968 • *Arthrobotrys candida* (Nees : Fr.) S. Schenck, W.B. Kendr. & Pramer - Can. J. Bot. **55**: 982. 1977 • *Dactylella candida* (Nees : Fr.) de Hoog & Oorschot - Stud. Mycol. **26**: 102. 1985 • *Monacrosporium candidum* (Nees : Fr.) Xing-Z. Liu & K.-Q. Zhang - Mycol. Res. **98**: 864. 1994 • *Golovinia capitulopaga* Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 169. 1979 (replacing *Dactylaria candida* sensu Drechsler non Nees, nom. inval., Art. 37 ICBN).
= *Dactylaria sclerohypha* Drechsler - Mycologia **42**: 57. 1950.
? = *Monacrosporium chinuanum* Xing-Z. Liu & K.-Q. Zhang, Mycol. Res. 98: 863. 1994.

Typification: Iconotype (Mycologia **42**: 43, 47). [p. 73]
Epitype: CBS 326.94 (= A.R. 9323), dried culture preserved in CBS.

Published descriptions: Drechsler (1937); Peach (1950); Cooke and Satchuthananthavale (1965); Ruokola and Salonen (1967); Rifai (1968); Dowsett and Reid (1977 b, c - trapping organs); Srivastava and Dayal (1984); Gray (1984).

Characteristics:
Conidiophores 150-300 µm high, bearing a cluster of 3-10 conidia on the tip, each on a stubby denticle (2-12 µm in length, Drechsler, 1937). Conidia spindle-shaped, (29-)35-50(-56) x (7-)8-9.5(-11) µm, commonly inequidistantly

four-septate. Chlamydospores in chains, 8-15 x 3-13 µm (Drechsler, 1950). Trapping nematodes by means of stalked knobs and/or non-constricting rings.

Material examined:
CBS 200.50 (= IMI 36115), (received as *D. candida*), from decaying leaf in a pond, UK, M. Peach.
CBS 220.54 (received as *D. candida*), A.J. Juniper, det. S.M. Dixon.
CBS 546.63, from soil, La Bresse, France, isol./det. R.C. Cooke; not producing trapping organs, not sporulating.
CBS 757.85 (= ATCC 28924).
A.R. 893, from dead stem of *Plantago lanceolata*, Berlin, Aug. 1989.
A.R. 8911, from dead stem of *Poa annua*, Berlin, Aug. 1989.
CBS 217.92 (= A.R. 9115), from soil in a warm greenhouse, Botanic Garden, Berlin-Dahlem, 4 Feb. 1991.
A.R. 9141, from soil (mangrove) in a warm greenhouse, Botanic Garden, Berlin-Dahlem, 30 Aug. 1991.
A.R. 9145, from soil in a cold greenhouse, Botanic Garden, Berlin-Dahlem, 30 Aug. 1991.
CBS 325.94 (= A.R. 9226), from soil of a laurel wood, Las Mercedes, Tenerife, coll./isol. G. Lysek, 1989.
CBS 326.94 (= A.R. 9323), from bark of *Sorbus torminalis*, Botanic Garden, Berlin-Dahlem, 22 Aug. 1993.
A.R. 9324, from leaf litter (*Genista spec.*), Botanic Garden, Berlin-Dahlem, 22 Aug. 1993.
CBS 327.94 (= A.R. 9325) and A.R. 9336, from dead twig (*Catalpa bignonioides*), Botanic Garden, Berlin-Dahlem, 22 Aug. 1993.
CBS 328.94 (= L.P. 9029), from soil under pasture, Sweden, coll./isol. L. Persmark, 9 May 1989.

Discussion:
Nees's fungus is documented only by an illustration (Syst. Pilze Schw. **58**: Taf. 2). No material could be found in the herbaria of E, L, CM (Pittsburg, no answer), and STR. Rejection of the name is proposed (Gams and Rubner, 1996; see Chapter 1). [p. 74]
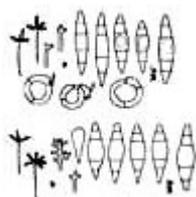
Fig. 32
Monacrosporium haptotylum; a. CBS 326.94 on CMA:2 (11 d) and WA+N (11 d). Habit sketch of conidiophores, conidiophore tips, conidia, and non-constricting rings; b. CBS 325.94 on CMA:2 (9 d) and WA+N (22 d). Habit sketch of conidiophores, conidiophore tips and conidia.

Drechsler (1950) distinguished *D. haptotyla* from *D. candida* by the less capitate conidial head and the lack of non-constricting rings. My own isolates of '*D. candida*', which at first had developed non-constricting rings, did not form them after a further [p. 75] transfer later (after some weeks of permanent culture); they also did not always sporulate abundantly, and only showed three or four conidia per conidiophore.

The possible synonymy of *D. haptotyla* with *D. sclerohypha* was also expressed by De Hoog and Van Oorschot (1985). Drechsler (1950) distinguished *D. sclerohypha* from the other two species by the formation of chlamydospores. Chlamydospores seem to be of low taxonomic value (as discussed in Chapter 4.4, p. 13).

18. Monacrosporium heterosporum (Drechsler) Subram. - Fig. 33.

Dactylella heterospora Drechsler - Mycologia **35**: 347. 1943 • *Monacrosporium heterosporum* (Drechsler) Subram. - J. Indian bot. Soc. **42**: 293. 1963 • *Golovinia heterospora* (Drechsler) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 172. 1979.

Typification: Iconotype (Mycologia **35**: 348, 350).

Published descriptions: Soprunov (1958; p. 110); Duddington (1951); Matsushima (1987).

Characteristics (after Drechsler, 1943)**:** Macroconidiophores simple, occasionally branched, mostly 200-500 µm high, bearing a single conidium on the tip (sometimes, through repeated elongation, one or two additional conidia). Macroconidia (from pure culture and from nematode-infested culture) ellipsoidal, 35-40-47 x 13-16.5-20 µm, two-septate. Microconidiophores often 15-25 µm long, with a geniculate rhachis, bearing 5-15 conidia on spurs (1-10 µm long). Microconidia cylindrical, curved and somewhat allantoid, 23-31.3-40 x 5.3-6.8-8 µm, one-septate. Chlamydospores regularly formed, often 15-30 x 15-20 µm (median cells), yellowish, in chains. Trapping nematodes by means of constricting rings.

Discussion:
Drechsler described conidiophores 'of the taller and more frequent type' and 'of the smaller type'. This smaller and less frequent type of conidia can be called microconidia. The shape of (macro)conidia of *M. heterosporum* is not very typical of *Monacrosporium*. However, no new combinations are proposed in cases where the generic identity is equivocal.

19. Monacrosporium inquisitor (Jarow.) Xing-Z. Liu & K.-Q. Zhang - Fig. 34.

Dactylella inquisitor Jarow. - Acta mycol. **7**: 4. 1971 • *Monacrosporium inquisitor* (Jarow.) Xing-Z. Liu & K.-Q. Zhang - Mycol. Res.

Typification: Iconotype (Acta mycol. **7**: 4, Fig. 1-8).

Characteristics (after Jarowaja, 1971)**:** Conidiophores up to 360 µm high, bearing a single conidium on the tip. Conidia spindle-shaped, 50-55-65 x 18-19-24 µm, mostly three-septate. Chlamydospores not observed. Trapping nematodes by means of constricting rings. [p. 76]

Fig. 33
Drechsler's original illustration (iconotype) of *Monacrosporium heterosporum* (Drechsler, 1943). Macroconidiophores, macroconidia, geniculate microconidiophores, microconidia, and (un)branched chlamydospore chains from pure culture on cornmeal agar. (Reproduced by permission of the Mycological Society of America). [p. 77]

Discussion:
The delimitation from other ring-forming species of *Monacrosporium* is difficult to work out in the absence of living or dried material.

Fig. 34
Monacrosporium inquisitor, original illustration from Jarowaja (1971). Conidiophore, conidia, constricting rings, and trapped nematode.

20. Monacrosporium iridis (Ts. Watan.) A. Rubner & W. Gams,*comb. nov.* - Fig. 35.

Basionym: *Trinacrium iridis* Ts. Watan. - Mycologia **84**: 794. 1992 • *Dactylella iridis* (Ts. Watanabe) K.Q. Zhang, Xing Z. Liu & L. Cao - Mycosystema **7**: 112. 1994. See also Nakagiri (1996).
= *Dactylella ramiformis* X.-Z. Liu & W.-F. Qiu - Mycol. Res. **97**: 359. 1993.

Typification: Holotype preserved at FFPRI under number TW 82-567.
Ex-type culture: CBS 686.94 = IFO 32554.
Dactylella ramiformis: Isotype preserved at HMAS under number 62571.
Ex-type culture: CBS 166.95 = IFO 32587.

Characteristics (after Watanabe, 1992 - measurements taken from PDA)**:** Macroconidiophores simple, (10-)62.5-117.5 µm high, bearing a single conidium on the tip. Macroconidia elongate-fusiform, 47.5-155 x 7.5-16.3 µm, four- to ten-septate, simple or radiately branched, rendering two or three conidial arms (branches). Arms tapering at the end, 13.7-95 x 5-12.5 µm, one- to five-septate. Microconidiophores developed from hyphae or from macroconidia, simple or branched, 37.5-225 µm high, bearing microconidia on denticles. Microconidia cylindrical, fusiform, obclavate, 20-47.5 x 3-5.3 µm, zero- or one-septate. Chlamydospores in chains, globose or subglobose, 10-15 µm in diameter. Trapping nematodes by means of three-dimensional networks (Nakagiri, 1996).

Material examined:
TW 82-567 (ST), from *Iris* roots, Wakayama, Japan; dry cultures without conidia. Living culture CBS 686.94. [p. 78]
HMAS 62571 (IT), from rhizosphere of *Triticum aestivum*, near Beijing, Apr. 1989; permanent slide, in a poor condition. The living culture CBS 166.95 remained sterile.

Fig. 35
Monacrosporium iridis, rearranged illustration from Watanabe (1992). Conidiophores, (branched) macroconidia, microconidiophores, microconidia, and chlamydospore chain. (Reproduced by permission of the Mycological Society of America).

Discussion:
Branched conidia have not been observed before in *Monacrosporium*. Only in *M. doedycoides* a few somewhat branched conidia were seen (Fig. 23 a); they were considered as a sign of degeneration as they had not been described for that species and were not found in the other sporulating isolate of *M. doedycoides*. The biological and taxonomic significance of branching in *M. iridis* remains open. Branched conidia would facilitate aquatic dispersal as in Ingoldian hyphomycetes. Even if the branching was not of taxonomic value, *M. iridis* is well-delimited by its tall conidia comparable only to those of *M. multiforme* (among the network-forming species), the latter being more slender (4-7.5 µm diam.). The observation of conidia measuring 38-80-116(-145) x 7.5-12-14 µm in CBS 773.84 of the latter species renders the distinction less certain.

Although *Dactylella ramiformis* could not be examined in a good condition, it is very likely to be synonymous with *M. iridis*. The branched conidia (16 % of the macroconidia), [p. 79] the great length of macroconidia (98-119-141 µm) and the existence of microconidia (Liu and Qiu, 1993) in *D. ramiformis* speak for the identity of the two species. Both species were isolated from rhizospheres.

21. Monacrosporium leptosporum (Drechsler) A. Rubner, *comb. nov.* - Fig. 36.

Basionym: *Dactylella leptospora* Drechsler - Mycologia **29**: 507. 1937 • *Dactylosporium leptosporum* (Drechsler) Mekht. - Mikol. Fitopatol. **1**: 277. 1967 • *Dactylellina leptospora* (Drechsler) M. Morelet - Bull. Soc. Sci. Nat. Archéol. Toulon Var **178**: 6. 1968.
= *Dactylaria dasguptae* S.K. Shome & U. Shome [as '*dasguptaii*'] - Mycopath. Mycol. appl. **30**: 216. 1966 [nom. inval., Art. 37 ICBN].
= *Kafiaddinia fusarispora* Mekht. - Mikol. Fitopatol. **12**: 8. 1978.

Typification: Iconotype (Mycologia **29**: 505).
Epitype: ATCC 36915 = CBS 560.92, dried culture in herb. CBS.

Published descriptions: Matsushima (1971); Saikawa (1985 - trapping organs).

Characteristics (after Drechsler, 1937)**:** Primary conidiophores 75-225 µm high, mostly simple, bearing a single conidium on the tip, occasionally another conidium on a short branch near the apex. Primary conidia mostly straight, elongate fusoid or cylindrical 40-105 x 4-5.8 µm, five- to fifteen-septate; conidia sometimes giving rise to one or two globose knobs mostly on scarcely differentiated distal prolongations, more rarely on lateral stalks. Secondary conidiophores often produced by primary conidia, 50-120 µm high. Secondary conidia 25-50 x 4-5.8 µm, three- to eight-septate. Chlamydospores not observed. Trapping nematodes by means of stalked knobs and non-constricting rings.

Material examined:
ATCC 36915 = CBS 560.92 (type isolate of *D. dasguptae*), from soil, G. L. Barron (No. 1046).

Discussion:
The species is well delimited by its long conidia and the two types of trapping organs, though Drechsler did not describe stalked knobs arising from mycelial hyphae, only from mature conidia. *Dactylaria dasguptae* (described without indication of a holotype) is regarded as a synonym of *M. leptosporum* for the following reasons: the reproductive structures are very similar to *M. leptosporum*. The more intensive branching of the conidiophore of *D. dasguptae* does not seem to justify the erection of a new species, nor does the occurrence of an additional trapping organ. ATCC 36915 produced conidiophores with one or two small branches-just as drawn by Drechsler for *M. leptosporum* (1937, his fig. 11, K, J and Q). The instability of non-constricting ring production is well demonstrated with this strain: sticky knobs on long stalks were produced, but no non-constricting rings.

   K. fusarispora is also regarded as a synonym of *M. leptosporum*. The genus *Kafiaddinia* with the type species *K. fusarispora* was erected by Mekhtieva (1979) in [p. 80] order to replace *Dactylosporium* Mekht. (type species: *D. leptosporum* (Drechsler) Mekht.). Micro- and macroconidia of Mekhtieva's fungus are elongate fusiform, with about the same length and width and the same number of septa as indicated by Drechsler for *M. leptosporum*, though more strongly curved according to her illustration. Furthermore they also trap nematodes by means of long stalked adhesive knobs and non-constricting rings.
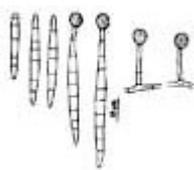
Fig. 36
Monacrosporium leptosporum, ATCC 36915 on CMA:2 (18 d, 32 d). Conidia, partly with adhesive knobs; stalked adhesive knobs formed on the hyphae.

22. Monacrosporium lobatum (Dudd.) A. Rubner, *comb. nov.* - Fig. 37.

Basionym: *Dactylella lobata* Dudd. - Trans. Br. mycol. Soc. **34**: 489. 1951.

Typification: Holotype IMI 49143.
Epitype: CBS 329.94 (= A.R. 9340), (dried culture preserved in herb. CBS).

Published descriptions: Soprunov (1958; p. 112); Gray and Duff (1982).

Characteristics (from Duddington, 1951)**:** Conidiophores 70-120 µm high, simple, carrying a single conidium on the tip. Conidia cylindrical to clavate, 38-48-55 x 8-10-12 µm, commonly three-septate, sometimes bearing one or two, often lateral, adhesive knobs. Chlamydospores not observed. Trapping nematodes by means of unstalked adhesive knobs. These knobs can proliferate in older cultures (on nematode-infested WA) and form lobed branches which are often forked; sometimes these proliferations join together to form loops.

Material examined:

IMI 49143 (T), from *Dicranella heteromalla*, Wimbleton Common, London, May 1950; dried material (pure culture).
CBS 227.54, isol. A.J. Juniper, det. S. Dixon, UK; not forming trapping organs, not sporulating. [p. 81]
CBS 228.54, isol. A.J. Juniper, det. C.L. Duddington; not forming trapping organs, not sporulating.
CBS 329.92 (= A.R. 9340), from rabbit dung, Grunewald, Berlin, Oct. 1993.

Discussion:
Apart from slightly longer conidiophores, indicated by Duddington as reaching 250 µm, there is no doubt of the identity of CBS 329.94 with Duddington's fungus.
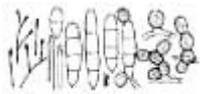
Fig. 37
Monacrosporium lobatum, CBS 329.94 on CMA:2 (8 d, 21 d) and WA+N (11 d). Habit sketch of conidiophores, conidiophore tips, conidia, and proliferating adhesive knobs.

23. Monacrosporium lysipagum (Drechsler) Subram. - Fig. 38.

Dactylella lysipaga Drechsler - Mycologia **29**: 503. 1937 • *Monacrosporium lysipagum* (Drechsler) Subram. - J. Indian bot. Soc. **42**: 293. 1963 • *Golovinia lysipaga* (Drechsler) Mekht. - Mikol. Fitopatol. **1**: 277. 1967.

Typification: Iconotype (Mycologia **29**: 501).

Published descriptions: Matsushima (1971, 1975); Wimble and Young (1984 - infection process); Fritsch and Lysek (1992).

Characteristics (after Drechsler, 1937)**:** Conidiophores 125-250 µm high, bearing a single conidium on the tip, sometimes with an additional conidium produced on a short branch below the tip. Conidia spindle-shaped, somewhat acutely rounded at the apex, 28-40.5-55 x 9-11.5-14 µm, sometimes with two or three septa, but commonly four-septate. Chlamydospores not observed. Trapping nematodes by means of stalked knobs and non-constricting rings.

Discussion:
This species is somewhat intermediate between *M. haptotylum* and *M. ellipsosporum*. Similar with *M. haptotylum* arethe conidial shape and the long-stalked knobs (as one type of the trapping organs). The higher number of conidia [p. 82] produced in a loose capitate arrangement on the conidiophore tip and the more slender conidia (average width around 9 µm) of *M. haptotylum* contrast with *M. lysipagum*. *M. ellipsosporum* only bears a single conidium on the conidiophore tip, produces wider conidia (average about 15 µm), and short-stalked knobs.

Fig. 38
Drechsler's original illustration (iconotype) of *Monacrosporium lysipagum* (Drechsler, 1937). Conidiophores, conidia (germinating), non-constricting rings and stalked knobs, trapped nematodes (*Rhabditis dolichura*). (Reproduced by permission of the Mycological Society of America). [p. 83]

24. Monacrosporium mammillatum (S.M. Dixon) R.C. Cooke & C.H. Dickinson - Fig. 39.

Dactylella mammillata S.M. Dixon - Trans. Br. mycol. Soc. **35**: 144. 1952 • *Monacrosporium mammillatum* (S.M. Dixon) R.C. Cooke & C.H. Dickinson - Trans. Br. mycol. Soc. **48**: 622. 1965 • *Golovinia mammillata* (S.M. Dixon) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 159. 1979.

Typification: Holotype preserved in K.
Epitype: CBS 304.94 (= A.R. 9332), dried culture preserved in CBS.

Published descriptions: Soprunov (1958; p. 112); Gray (1983).

Characteristics:
Conidiophores 150-250 µm high, bearing a single conidium on the tip. Conidia ellipsoidal to spindle-shaped, with a blunt apex, 29-35-44 x 9-11-14 µm, three- or four-septate. Chlamydospores not observed. Trapping nematodes by means of short-stalked knobs (stalks unicellular).

Fig. 39
Monacrosporium mammillatum, a. CBS 588.91 on CMA:2 (27 d). Conidia. b. type specimen in KOH. Conidia, at the same scale.

Material examined:
Type material, a dried culture, from rotting wood of *Ulmus* spec., near Eynsham, Oxford, UK, Sept. 1950, S.M. Dixon.

CBS 229.54 (ex-type culture), as above; not sporulating.
CBS 486.63 (= MUCL 1657) (received as *D. lysipaga*), from decaying moist wood, Ottawa River, Ontario, Canada, 1960, G.L. Hennebert.
CBS 588.91 (= A.R. 919), from soil in cold greenhouse, Botanic Garden, Berlin-Dahlem, Feb. 1991. [p. 84]
CBS 304.94 (= A.R. 9332), from leaf litter (*Larix decidua*), Botanic Garden, Berlin-Dahlem, 22 Aug. 1993.

Discussion:
In the type specimen the conidia measure 15-23 x 6-9 µm. They are obovoid to clavate and three-septate; no trapping organs were observed. This deviates considerably from Dixon's original measurements and her drawings. (The type culture does not sporulate, but produces stalked knobs.) Dixon emphasized the more rounded outline and blunt tip of the conidia of *M. mammillatum* in contrast to the angular outline of the conidia in *M. ellipsosporum*. She described the conidia of the former as mostly five-celled, but occasionally four- and three-celled. Her drawings, however, show four-septate conidia with a more angular apical cell and three-septate conidia with a blunt apical cell.

CBS 486.63 forms almost exclusively three-septate conidia measuring 29-32-35 x 8.5-10-12 µm. CBS 304.94 (epitype) also shows almost only three-septate conidia measuring 30-36-42.5 x 9-11-13 µm. There is obviously a need for a taxon covering isolates with three-septate, blunt conidia of this size, and therefore *M. mammillatum* is retained in this sense.

25. Monacrosporium megalosporum (Drechsler) Subram. - Fig. 40.

Dactylella megalospora Drechsler - Mycologia **46**: 769. 1954 • *Monacrosporium megalosporum* (Drechsler) Subram. - J. Indian bot. Soc. **42**: 293. 1963 • *Golovinia megalospora* (Drechsler) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 155. 1979.

Typification: Iconotype (Mycologia **46**: 772, 774).

Published descriptions: Soprunov (1958; p. 111); Cooke and Dickinson (1965); Srivastava and Dayal (1982); Esser *et al.* (1990); Fritsch and Lysek (1992).

Characteristics (after Drechsler, 1954)**:** Conidiophores from pure culture 150-250 µm high, with one to five almost perpendicular denticles (10-40 µm long), on which additional conidia are formed. Conidiophores from nematode-infested substratum usually 350-450 µm high, bearing a single conidium on the tip. Conidia broadly fusoid or elongate-ellipsoidal or obovoid, 40-75 x 18-35 µm, commonly two- to five-septate. Conidia from nematode-infested substrata frequently 55-75 x 23-35 µm, four-septate. Chlamydospores not observed. Trapping nematodes by means of three-dimensional networks.

Discussion: Drechsler mentioned *M. thaumasium*, *M. psychrophilum* and *M. eudermatum* as the closest known relatives of *M. megalosporum*, but conidial size is definitely larger than in any of these taxa. No living culture is now available.

26. Monacrosporium multiforme (Dowsett, J. Reid & Kalkat) A. Rubner, *comb. nov.* - Fig. 41.

Basionym: *Dactylella multiformis* Dowsett, J. Reid & Kalkat - Mycologia **76**: 563. 1984.

Typification: Iconotype (Mycologia **76**: 564, 565).
Ex-type culture: CBS 773.84 [p. 85]

Fig. 40
Drechsler's original illustration (iconotype) of *Monacrosporium megalosporum* (Drechsler, 1954). Conidiophores, conidia, adhesive networks, and trapped nematodes from pure and nematode-infested cultures. (Reproduced by permission of the Mycological Society of America). [p. 86]

Characteristics (after Dowsett *et al.*, 1984)**:** Primary conidiophores 80-220 µm high, producing a single conidium on the tip. Primary conidia 35-90.5(-116) x 4-7.5(-14) µm, four- to twelve-septate, inequidistantly septate. Secondary conidiophores arising from primary conidia, up to 120 µm high. Secondary conidia clavate to cylindric-clavate, 20-25 x 5 µm, unequally one-septate. Tertiary conidiophores arising from secondary conidia, up to 40 µm high. Tertiary conidia clavate, 15-17 x 5 µm, one-celled. Chlamydospores present in older cultures, in chains. Trapping nematodes by means of three-dimensional networks.
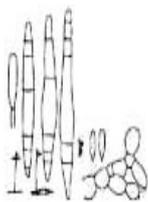
Fig. 41
Monacrosporium multiforme, CBS 773.84 on CMA:2 (27 d, 60 d) and WA+N (60 d). Macroconidia, habit sketch of microconidiophores arising from a macroconidium, microconidia, and chlamydospore chain.

Material examined:
CBS 773.84 (T), from marsh soil, University Field Station, Delta Marsh, Manitoba, Canada, isol. J. Reid.

Discussion:
Conidial measurements given by Dowsett *et al.* (1984, copied above) differ from those measured in the type-culture: 38-80-116 (even up to 145 µm) x 7.5-12-14 µm, three- to six-septate, cylindrical to fusiform. Age and media on which the fungus was cultivated were different, too. Dowsett *et al.* (1984) grew the fungus for 7 d on potato-carrot agar plus nematodes. In this study chlamydospores were observed on CMA:2 after 62 d, microconidia appeared on WA plus nematodes after 60 d, and conidia were drawn from CMA:10 after 27 d. The fragmentation of conidia into arthrospore-like parts as illustrated and described by Dowsett *et al.* was not seen. The trapping organs, induced by nematodes, were similar to the hyphal branches of *M. gephyropagum*, some of them coiling in many loops (Fig. 41). Normal three-dimensional networks, as indicated in the original description, were not observed. [p. 87]

27. Monacrosporium mutabile R.C. Cooke - Fig. 42.

Monacrosporium mutabile R.C. Cooke [as '*mutabilis*'] - Trans. Br. mycol. Soc. **53**: 318. 1969 • *Golovinia mutabilis* (R.C. Cooke) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 161. 1979.

Typification: Holotype IMI 138221.

Characteristics (after Cooke, 1969): Conidiophores bearing a single conidium. Conidia from nematode-infested (CMA) culture ellipsoidal, 50-60 x 16-17.5 µm, invariably four-septate. Conidia from pure culture (CMA) different in shape and size: 37.5-50 x 12.5-15 µm, sometimes three-septate, frequently malformed (Cooke, 1969). Chlamydospores not observed. Trapping nematodes by means of knobs (about 5 µm in diameter), supported by a two-celled stalk; stalks frequently branched at the base.

Material examined:
IMI 138221, dried culture from OA, from soil near Nafanua, Western Samoa, R.C. Cooke, Feb. 1969.

Discussion:
The species seems to be well-delimited from other four-septate *Monacrosporium*-species by its characteristic adhesive knobs borne on branched stalks. The type material examined showed some discrepancies with Cooke's description of the conidia. Conidia (from OA, permanent slide) measured 41.5-55-62 x 13.5-17.5-19 µm; in an own preparation made with KOH and phloxin B, however, they were 48-57.5 x 14-17.5 µm, mostly four-septate and sometimes five-septate. Trapping organs were not observed.
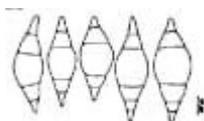

Fig. 42
Monacrosporium mutabile, IMI 138221, type specimen, in KOH. Conidia. [p. 88]

28. Monacrosporium obtrulloides Castaner - Fig. 43.

Monacrosporium obtrulloides Castaner - Can. J. Bot. **46**: 764. 1968.

Typification: The type was said to be preserved at WARM under No. 83il, but no answer was obtained on a request; MO does not preserve the material.

Characteristics (after Castaner, 1968)**:** Conidiophores 80-140 µm high, bearing a single conidium on the tip. Conidia obtrulloid-fusiform, 39.5-43.5-46 x 10.5-14-17.5 µm, two-septate. Chlamydospores not observed. Trapping nematodes by means of constricting rings.

Discussion:
The species is close to *M. bembicodes*, as already mentioned by Castaner, but differs from it by two-septate and more slender conidia.
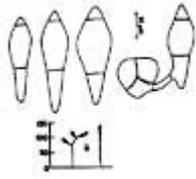
Fig. 43
Monacrosporium obtrulloides, original illustration from Castaner (1968). Habit sketch of conidiophores, conidia (one conidium with a constricted ring).

29. Monacrosporium parvicolle (Drechsler) R.C. Cooke & C.H. Dickinson - Fig. 44.

Dactylella parvicollis Drechsler - Sydowia **15**: 13. 1962 ('1961') • *Monacrosporium parvicolle* (Drechsler) R.C. Cooke & C.H. Dickinson [as '*parvicollis*'] - Trans. Br. mycol. Soc. **48**: 622. 1965 • *Golovinia parvicollis* (Drechsler) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 162. 1979.

Typification: Iconotype (Sydowia **15** - Plate IV, V).
Ex-type culture: CBS 219.61 (= ATCC 14447), dried culture in herb. CBS.

Published descriptions: Cooke (1967 a); Jarowaja (1968); Lysek and Kürschner (1987, as *M. gephyropagum*); Fritsch and Lysek (1992).

Characteristics (after Drechsler, 1962)**:** Conidiophores mostly 130-290 µm high, bearing a single conidium. Conidia commonly spindle-shaped, rounded on the tip, [p. 89] narrowly truncate at the base, 35-45 x 8-14 µm, mostly four-septate. Chlamydospores not observed. Trapping nematodes by means of (short-stalked) knobs which can grow out and form loops.
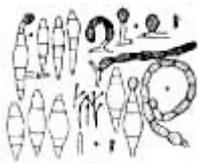

Fig. 44.
Monacrosporium parvicolle; a. CBS 219.61 (ex-type culture) on CMA:2 (16 d) and CMA:2+N (75 d). Conidia (one conidium germinating with an adhesive knob. and proliferating (stalked) adhesive knobs; b. CBS 314.94 on CMA:2 (8 d). Habit sketch of conidiophores, conidiophore tip, and conidia; c. L.P. 9026 on CMA:2 (11 d). Conidia (one conidium germinating with an adhesive knob) and adhesive knob proliferating to form a loop.

Material examined:
CBS 219.61 (T), from leaf litter, near Durango, Colorado, USA, C. Drechsler.
CBS 429.91 (= A.R. 8915), from dead grass, Berlin, Dec. 1989.
A.R. 8919 and 8923, from deciduous leaf litter, Berlin, Feb. 1990 and Dec. 1989..
CBS 590.91 (= A.R. 9025), from soil, Berlin, Dec. 1990.
CBS 312.94 (= A.R. 921), from soil, Yosemite National Park, California, U.S.A., Dec. 1991, coll. L. Smith. [p. 90]
CBS 313.94 (= A.R. 9310), from horse dung, National Park Cotopaxi, Ecuador, 16 March 1993.
CBS 314.94 (= A.R. 9330), from leaf litter, Botanic Garden, Berlin-Dahlem, 22 Aug. 1993.
L.P. 9026, from field soil (clay), Sweden, 9 May 1989, coll./isol. L. Persmark.

Discussion:
The type culture does not sporulate well. Conidia are slender, 29-47 x 6-88-10.5 µm, three- and four-septate. Adhesive knobs develop spontaneously from the hyphae on short stalks and readily grow out; mature conidia may also develop a knob at the apical cell. The (average) length and width of conidia from CBS 313.94 and 314.94 are: 42.5-48.5-56 x 11.5-14-16 µm (three- and four-septate) and 35-42-50.5 x 11.5-12.5-15 µm (mostly three-septate), respectively. If all strains with the conspicuous type of trapping organ described above and pictured in figure 45 and with slender, spindle-shaped conidia are to be accepted as conspecific, a considerable variability of this species must be taken into account.

30. Monacrosporium phymatopagum (Drechsler) Subram. - Fig. 45.

Dactylella phymatopaga Drechsler - Mycologia **46**: 775. 1954 • *Monacrosporium phymatopagum* (Drechsler) Subram. - J. Indian bot. Soc. **42**: 293. 1963 • *Golovinia phymatopaga* (Drechsler) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 165. 1979.
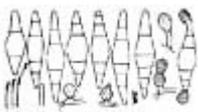
Fig. 45
Monacrosporium phymatopagum, CBS 315.94 on CMA:2 (8 d, 14 d). Habit sketch of conidiophores, conidiophore tip, conidia, one conidium with adhesive knobs arising from the apical and basal cells, and adhesive (stalked) knobs formed on the hyphae.

Typification: Iconotype (Mycologia **46**, 778).
Epitype: CBS 315.94 (= A.R. 9233), dried culture preserved in herb. CBS. [p. 91]

Published descriptions: Soprunov (1958; p. 112); El Amin (1980).

Characteristics (after Drechsler, 1954): Conidiophores 250-325 µm high, bearing a single conidium on the tip. Conidia usually spindle-shaped, truncate, and rather narrow at the base, rounded at the distal end, 40-49.2-60 x 11-14.4-18 µm, commonly four-septate. Chlamydospores not observed. Trapping nematodes by means of sessile knobs.

Material examined:
CBS 325.72, from greenhouse soil, Naaldwijk, det. H. Kaastra and W. Gams.
CBS 315.94 (= A.R. 9233), from moss, Berlin, 1992, coll./isol. S. Behnke.

A.R. 9313, from plantation soil, Province Pichincha, Ecuador, 8 March 1993.
CBS 317.94 (= L.P. 9027), from meadow soil, Sweden, 9 May 1989, coll./isol. L. Persmark.

Discussion:
The species closely resembles *M. ellipsosporum* with its solitary conidia, which are spindle-shaped and four-septate; however, conidia are much longer in *M. ellipsosporum*. According to Drechsler, *M. phymatopagum* differs from other species mainly by its unstalked knobs, which are obovoid rather than globose. The majority of isolates of this study produced knobs, which were not always sessile and tended to develop stalks up to 12 µm long (as in CBS 325.72, 315.94 and 317.94). Only A.R. 9313 developed unstalked knobs, its conidia being 56.5-62-68 x 13.5-15.5-17.5 µm.

31. Monacrosporium polybrochum (Drechsler) Subram. - Fig. 46.

Trichothecium polybrochum Drechsler - Mycologia **29**: 536. 1937 • *Dactylella polybrocha* (Drechsler) Mekht. - Dokl. Akad. Nauk Azerb. SSR **20**(6): 70. 1964 • *Monacrosporium polybrochum* (Drechsler) Subram. - Kavaka **5**: 96. 1977 • *Golovinia polybrocha* (Drechsler) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 137. 1979.

Typification: Iconotype (Mycologia **29**: 537).

**Published descriptions:** Mekhtieva (1964).
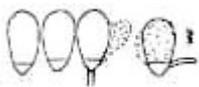
Fig. 46
Monacrosporium polybrochum, CBS 319.56 on CMA:2 (38 d) and CMA+N (24 d). Conidia with layer of mucus, damaged during preparation. [p. 92]

Characteristics (after Drechsler, 1937)**:** Conidiophores 275-400 µm high, bearing a single conidium. Conidia broadly obovoid, about 35 x 24 µm, one-septate, often enveloped in a hyaline layer of mucus. Chlamydospores not observed. Trapping nematodes by means of constricting rings.

Material examined:
CBS 319.56, from decayed wood, West Virginia University, Morgantown, Virginia, USA, H.L. Barnett; not forming trapping organs any more.

Discussion:
The generic classification of this species is equivocal. The regularly didymosporous conidia suggest *Arthrobotrys*, the monoblastic conidiophores suggest *Monacrosporium*.

32. Monacrosporium psychrophilum (Drechsler) R.C. Cooke & C.H. Dickinson - Fig. 47.

Dactylaria psychrophila Drechsler - Mycologia **36**: 161. 1944 • *Monacrosporium psychrophilum* (Drechsler) R.C. Cooke & C.H. Dickinson - Trans. Br. mycol. Soc. **48**: 622. 1965 • *Geniculifera psychrophila* (Drechsler) Rifai - Reinwardtia **7**: 357. 1968 • *Golovinia psychrophila* (Drechsler) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 151. 1979.

Teleomorph: **Orbilia auricolor** (Bloxam ex Berk.) Sacc. - Syll. Fung. **8**: 625. 1889 - Fig. 48.

Mollisia auricolor Bloxam ex Berk. - Ann. Mag. Nat. Hist. Ser. 3, **15**: 346. 1865 • *Calloria auricolor* (Bloxam ex Berk. & Broome) Phillips - Manual of British Discomycetes: 334. 1887.
= *Orbilia curvatispora* Boud. - Bull. Soc. Mycol. France **4**: 80. 1888
= *Orbilia tremulae* Velen. - Monographia Discomycetum Bohemiae: 92. 1934, and other synonyms, teste Spooner (1987).

Typification: *M. psychrophilum*: Iconotype (Mycologia **36**: 162 C-F, 165).
Epitype: CBS 548.63, dried culture preserved in herb. CBS.
Orbilia auricolor: Holotype in K, as indicated and examined by Spooner (1987).

Published descriptions: Duddington (1951); Sheperd (1956); Soprunov (1958; p. 103); Gray (1985 a); Fritsch and Lysek (1989).

Characteristics of the teleomorph (CBS 319.94): Mature apothecia deviating from normal *Orbilia* apothecia by strongly convex warted hymenia. Asci measuring 45-58 x 3.5-4.2 µm. Ascospores tear-shaped, 7.5-13 x 1-1.3 µm. An ellipsoid refractive spore body is attached to the spore apex by a thin thread. Three to five of the lower spores inversely oriented within asci. Paraphyses slightly inflated at the apex. Cortical cells of ectal excipulum terminated by 2 to 6 µm high glassy caps (after Baral, ined.).

Characteristics of the anamorph (after Drechsler, 1944 a): Conidiophores mostly 150-500 µm high, bearing a single conidium on the tip or up to three additional conidia on perpendicular, up to 35 µm long branches. Conidia ellipsoidal or fusiform-ellipsoidal, rounded at the distal end and somewhat truncate at the proximal end, [p. 93]

46-62.3-71 x 21-24.7-29 µm, mostly three- or four-septate. Microconidia sometimes formed in ageing cornmeal agar cultures, 14-35 x 4.8-7.5 µm, without or with one median septum. Chlamydospores in chains, thick-walled, smooth, yellowish. Trapping nematodes by means of three-dimensional networks.
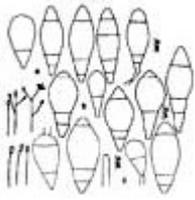
Fig. 47
Monacrosporium psychrophilum; a. CBS 548.63 on CPA (21 d). Conidia; b. CBS 318.94 on CMA:2 (12 d, 21 d). Habit sketch of conidiophores and conidia; c. L.P. 9203 on CMA:2 (14 d). Habit sketch of conidiophores, conidiophore tip, and conidia [p. 94].

Fig. 48
Orbilia auricolor as developed in a culture of *Monacrosporium psychrophilum* CBS 319.94 (original kindly supplied by H.-O. Baral). a. apothecia; b. cortical cells of ectal excipulum; c. paraphyses; d. ascus and enlarged ascus tip; e. ascospores and enlarged ascospore apex. Scale bars = 0.5 mm (a), 5 µm (b-e).

Material examined:
CBS 547.63, from soil, U.K., R.C. Cooke; does not form trapping organs, does not sporulate.
CBS 548.63, from wheat-field soil, Germany, coll./isol./det. W. Gams.
CBS 318.94 (= A.R. 938), from soil, Ecuador, 6 March 1993 (resembling A.R. 937 = CBS 316.94, *M. elegans*).
CBS 319.94 (= A.R. 9312), from soil, Hacienda Cienega, Ecuador, 16 March 1993.
L.P. 9203, from soil, Sweden, 1992, coll./isol. L. Persmark.
L.P. 9031, from the rhizosphere (sandy), Sweden, 10 Aug. 1990, coll./isol. L. Persmark.

Discussion:
This anamorph-species was not commonly isolated, although, according to the literature (Gray; 1985 a, b) it does not seem to be rare. Its preference for low temperatures has been discussed earlier. Morphologically the fungus resembles *M. reticulatum* on one side and *M. elegans* on the other. If the middle or penultimate cell of the conidium does not exceed the other cells markedly in width, the delimitation from *M. reticulatum* is difficult (L.P. 9203, Fig. 47 c). If the middle or penultimate cell does exceed the other cells significantly ('inflated' cell, much curved), the fungus is closer to *M. elegans* (CBS 319.94). [p. 95]

For the production of ascomata CBS 319.94 was kept at 15 and 25 ºC on different types of agar (WA, PCA, CMA:2, with and without oat chaff, and MEA) and observed for five months. After two months the first apothecia were visible on the CMA:2 plates with oat chaff. Later on all other agar types fruitbodies were formed, but not on WA. Dried material is preserved at CBS.

33. Monacrosporium reticulatum (Peach) R.C. Cooke & C.H. Dickinson - Fig. 49.

Dactylella reticulata Peach - Trans. Br. mycol. Soc. **33**: 148. 1950 • *Monacrosporium reticulatum* (Peach) R.C. Cooke & C.H. Dickinson - Trans. Br. mycol. Soc. **48**: 622. 1965 • *Golovinia reticulata* (Peach) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 143. 1979.

Typification: Iconotype (Trans. Br. mycol. Soc. **33**: 150).
Ex-type culture: CBS 201.50, dried material preserved in CBS.

Characteristics (after Peach, 1950)**:** Conidiophores simple, only infrequently branched at the base, about 250 µm high, producing a single conidium on the apex. Conidia ellipsoid, with one of the middle cells being largest, 50-65 x 20-25 µm, mostly four-septate, sometimes five-septate. Chlamydospores present in older cultures, in chains or clusters, globose to subglobose, around 12 µm in diam. or about 15 µm in length. Trapping nematodes by means of three-dimensional networks.

Fig. 49
Monacrosporium reticulatum, CBS 201.50 on CMA:2 (48 d) and CPA (26 d). Habit sketch of conidiophores, conidia, chlamydospores in chain and cluster. [p. 96]

Material examined:
CBS 201.50, from decaying leaves of *Quercus petraea* and *Fagus sylvatica* var. *cuprea*, in a garden fountain, near Harpenden Common, Herts., UK, isol./det. M. Peach (M.P. 36114).

Discussion:
M. psychrophilum and *M. reticulatum* are similar in conidial size. Peach (1950) did not mention the former species as closely related. The pure (type-)culture, however, shows some differences with the original description: conidiophores sometimes branched near the apex, side branches long, conidiophore length up to 210 µm, conidia

47-70 (s.d. 7)-85 x 13-18 (s.d. 2.6)-25 µm (n = 60), three- to five-septate, mostly four-septate, chlamydospores in chains or clusters. Thus the delimitation from *M. psychrophilum* is rather sharp.

34. Monacrosporium robustum J.S. McCulloch - Fig. 50.

Monacrosporium robustum J.S. McCulloch - Trans. Br. mycol. Soc. **68**: 177. 1977.

Typification: Holotype preserved at BRIP under No. 11222.

Characteristics (after McCulloch, 1977)**:** Conidiophores 150-450 µm high, bearing a single conidium on the tip. Conidia spindle-shaped, 68-85 x 20-30 µm, three- to five-septate. Chlamydospores not known. Trapping nematodes by means of stout unicellular adhesive branches, 16-24 x 9-10 µm.

Material examined:
BRIP 11222 (T), from soil under *Rheum rhaponticum*, Mt. Tamborine, Queensland, Apr. 1968, coll. R. Colbran; dried culture.

Discussion:
The species is easily recognized by its large conidia and its characteristic trapping organs. The type material agrees well with the original description: conidia on average 77 x 23.5 µm, trapping organs one-celled and of characteristic size.
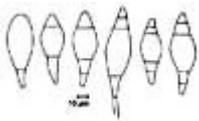

Fig. 50
Monacrosporium robustum, type specimen, in KOH. Conidia.

Fig. 51
Monacrosporium salinum, original illustration from Cooke & Dickinson (1965). Conidia from CMA-culture (a) and from RDA-culture (b). (Reproduced by permission of the British Mycological Society). [p. 97]

35. Monacrosporium salinum R.C. Cooke & C.H. Dickinson - Fig. 51.

Monacrosporium salinum R.C. Cooke & C.H. Dickinson - Trans. Br. mycol. Soc. **48**: 626. 1965 • *Golovinia salina* (R.C. Cooke & C.H. Dickinson) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 145. 1979.

Typification: Holotype in IMI, No. 109555 (apparently lost).

Published descriptions: Srivastava & Dayal (1982).

Characteristics (after Cooke & Dickinson, 1965)**:** Conidiophores
bearing a single conidium at the apex. Conidia (from CMA) fusiform-ellipsoidal, 32.5-52.5 x 12.5-17.5 µm, zero- to four-septate, but mainly three-septate. Chlamydospores not known. Trapping nematodes by means of three-dimensional networks.

Discussion:
This is one of the many network-forming species. The variation of conidial septation and the complete change of shape (and size) on different media makes this fungus difficult to identify.

36. Monacrosporium stenobrochum (Drechsler) Subram. - Fig. 52.

Dactylella stenobrocha Drechsler - Mycologia **42**: 10. 1950 • *Monacrosporium stenobrochum* (Drechsler) Subram. - J. Indian bot. Soc. **42**: 293. 1963 • *Golovinia stenobrocha* (Drechsler) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 171. 1979.

Typification: Iconotype (Mycologia **42**: 7).

Published descriptions: Soprunov (1958; p. 109).

Characteristics (after Drechsler, 1950)**:** Conidiophores 425-550 µm high, bearing a single conidium at the apex. Conidia elongate-ellipsoidal, sometimes slightly clavate, straight or curved, 34-56.5 x 12.5-16.5 µm, one- to three-septate. Chlamydospores not known. Trapping nematodes by means of constricting rings.

Discussion:

The broadly rounded conidia of *M. stenobrochum* are unusual in *Monacrosporium*. Therefore the species is very distinct.

37. Monacrosporium tentaculatum A. Rubner & W. Gams, *nom. nov.* - Fig. 53.

Replaced synonym: *Dactylella appendiculata* Anastasiou - Pacif. Sci. **18**: 202. 1964 • *Laridospora appendiculata* (Anastasiou) Nawawi - Trans. Br. mycol. Soc. **66**: 344. 1976 [non *Monacrosporium appendiculatum* (Mekht.) Xing.-Z. Liu & K.-Q. Zhang].

Typification: Holotype H 47 (herbarium Anastasiou), not seen.
Ex-type culture: CBS 206.64.

Published descriptions: Nawawi (1976). [p. 98]

Characteristics (after Anastasiou, 1964)**:** Conidiophores 50-400 μm high, bearing a single conidium on the tip. Conidia spindle-shaped, 57-87-108 x 9.3-14.5 μm, mostly inequidistantly four- to seven-septate, producing 1-4 lateral arms (10-136 x 2-3.5 μm) from the parabasal cells. Aquatic. Chlamydospores not known. Trapping nematodes by means of stalked knobs.

Material examined:
CBS 206.64 (syntype of *Dactylella appendiculata*), from leaves in water, Kokee stream, Na Pali Kona Reserve, Kauai, Hawaii, 30 Aug. 1961, C.J. Anastasiou; not sporulating.

Discussion:
The species is well-delimited against other knob-forming species of *Monacrosporium* by its long conidia, which are often curved when immature (Anastasiou, 1964) and still bent when mature, furthermore by the slender appendages deriving from the parabasal cells. In *M. acrochaetum* similar appendages have been interpreted as precocious germ tubes (Cooke, 1967 a), and the erection of the new genus *Drechslerella* Subram. based on this character was therefore rejected. In the case of *M. tentaculatum* the appendages are, however, concentrated on a specific point of the conidium. They are produced in considerable numbers (up to 7; Nawawi, 1976). They are likely to facilitate floating in the water as it is known for other aquatic hyphomycetes.

Nawawi (1976) placed the former *Dactylella appendiculata* in the newly erected genus *Laridospora* because of (its characteristic conidial morphology and) its semi-aquatic and non-predacious habit. The author did not mention whether he had specifically tested the fungus on nematode-trapping activities. When CBS 206.64 was grown (in 1991 and 1994) on WA to which *Turbatrix aceti* was added, it formed stalked knobs after three days in large numbers and all nematodes were trapped after a few days. Though the strain was grown on different media (WA, CMA:2, and leaves in water) and the CMA:2 cultures were floated with (sterile) tap water, it only developed sterile aerial hyphae, but never conidia.

Because *Golovinia appendiculata* Mekht. was recently transferred to *Monacrosporium* by Liu & Zhang (1994), a name change is necessary in spite of the doubtful identity of Mekhtieva's fungus (p. 105). The new epithet refers to the conidial appendages characteristic of the species.

38. Monacrosporium thaumasium (Drechsler) de Hoog & Oorschot - Fig. 54.

Dactylaria thaumasia Drechsler - Mycologia **29**: 522. 1937 • *Golovinia thaumasia* (Drechsler) Mekht. - Mikol. Fitopatol. **1**: 276. 1967 • *Candelabrella thaumasia* (Drechsler) Rifai - Reinwardtia **7**: 369. 1968 • *Arthrobotrys thaumasia* (Drechsler) S. Schenck, W.B. Kendr. & Pramer - Can. J. Bot. **55**: 984. 1977 • *Monacrosporium thaumasium* (Drechsler) de Hoog & van Oorschot - Stud. Mycol. **26**: 120. 1985.
= *Monacrosporium cystosporum* R.C. Cooke & C.H. Dickinson - Trans. Br. mycol. Soc. **48**: 623. 1965 • *Golovinia cystospora* (R.C. Cooke & C.H. Dickinson) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 146. 1979.
= *Monacrosporium globisporum* R.C. Cooke [as 'globosporum']- Trans. Br. mycol. Soc. **50**: [p. 99]
515. 1967 • *Golovinia globispora* (R.C. Cooke) Mekht. [as 'globospora'] - Khishchnye nematofagovye Griby-Gifomitsety: 144. 1979.
? = *Monacrosporium sinense* Xing-Z. Liu & K.Q. Zhang, Mycol. Res. 98: 863. 1994.

Fig. 52
Drechsler's original illustration (iconotype) of *Monacrosporium stenobrochum* (Drechsler, 1950). Conidiophores, conidia, constricting rings, and trapped nematodes (*Plectus* sp.). (Reproduced by permission of the Mycological Society of America). [p. 100]

Fig. 53
Monacrosporium tentaculatum, a. original illustration from Anastasiou (1964). Development of conidia, conidia with appendages, and chlamydospores. b. CBS 206.64 on WA+N (9 d). Stalked adhesive knobs.

Typification: Iconotype (Mycologia **29**: 519).
Syntype: CBS 176.37. Ex-type culture: ATCC 18498 = CBS 566.95 (dried culture in CBS).
M. cystosporum: Holotype preserved as IMI 109554 (not recognizable).
M. globisporum: Holotype preserved as IMI 121299 (apparently lost).

Published descriptions: Soprunov (1958; p. 101, 146); Sachchidananda and Krishnan (1971); El Amin (1980); Fritsch and Lysek (1992). [p. 101]
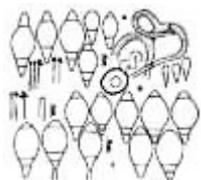

Fig. 54.
Monacrosporium thaumasium; a. CBS 176.37 (ex-type culture) on CMA:2 (21 d, 39 d) and CPA (21 d). Habit sketches of macro- and microconidiophores, macro- and microconidia, thick-walled chlamydospore, and spontaneously formed adhesive loops; b. CBS 321.94 on CMA:2 (11 d). Habit sketch of conidiophores, conidiophore tip, and macroconidia. c. ATCC 18498 on CMA:2 (26 d) and MEA (8 d). Conidia.

Characteristics: Conidiophores 150-420 µm high, bearing 2-10 small perpendicular branches (mostly 2-10 µm long; Drechsler, 1937). Conidia top-shaped, measuring 35-42-51 x 15-19-23 µm, most often inequidistantly three-septate. Microconidia elongate-obovoidal, about 17 x 5 µm, nonseptate. Chlamydospores present in older cultures, single, more or less globose. Trapping nematodes by means of three-dimensional networks. [p. 102]

Material examined:
CBS 176.37 (syntype of *M. thaumasium*), from decaying root of *Spinacia oleracea*, USA, coll./isol./det. C. Drechsler.
IMI 109554 (T of *M. cystosporum*), dried culture, from soil, Botanic Garden, Java, Bogor, 1966, R. C. Cooke; only contaminations could be detected.
ATCC 18498 (T of *M. globisporum*), from soil of permanent pasture, Cressbrook Dale, Derbyshire, UK, July 1966, R.C. Cooke.
CBS 132.42 (received as *M. bembicodes*), from nematodes on root of *Spinacia oleracea*, Netherlands; the culture forms three-dimensional networks instead of constricting rings.
CBS 128.83 (IMI 101312), U.K., det. C.L. Duddington; sporulates poorly.
CBS 770.85 (received as *Geniculifera eudermata*), W.D. Rosenzweig.
CBS 589.91 (= A.R. 9015), from soil, Berlin, 23 March 1990.
CBS 591.91 (= A.R. 917), from soil in warm greenhouse, Botanic Garden, Berlin-Dahlem, 4 Feb. 1991.
A.R. 9119, from soil, Thailand, Apr. 1991, coll. M. Knabe.
A.R. 9121, from soil of an orchid pot in warm greenhouse, Botanic Garden, Berlin-Dahlem, 24 Apr. 1991.
A.R. 9122, from soil in cold greenhouse, Botanic Garden, Berlin-Dahlem, 24 Apr. 1991.
CBS 320.94 (= A.R. 9126), from soil, Thailand, coll. M. Knabe, Apr. 1991.
CBS 321.94 (= A.R. 9137), A.R. 9130, A.R. 9132, and A.R. 928, from soil in warm greenhouse, Botanic Garden, Berlin-Dahlem, 30 Aug. 1991 and 17 March 1992.
CBS 322.94 (= A.R. 9139) and A.R. 9214, from soil in cold greenhouse, Botanic Garden, Berlin-Dahlem, 30 Aug. 1991 and 10 July 1992.
A.R. 927, from rhizosphere of orchid in warm greenhouse, Botanic Garden, Berlin-Dahlem, 17 March 1992.
CBS 323.94 (= A.R. 9329), from leaf litter of *Chamaecytisus pisiferus*, Botanic Garden, Berlin-Dahlem, 22 Aug. 1993.
CBS 324.94 (= A.R. 9334), from leaf litter of *Quercus ilicifolia*, Botanic Garden, Berlin-Dahlem, 22 Aug. 1993.

Table 8: Reproductive structures in some isolates of *M. thaumasium*

strain	hight	no. of con.	conidia	l : w	chlam.
CBS 770.85	150-415	8	36-45-51 x 17-19-21	2.36	+
CBS 320.94	200-360	6	39.5-44.5-50 x 17.5-20.5-22.5	2.20	-
CBS 321.94	215-350	3	35.5-39.5-43 x 16.5-19.5-22.5	2.03	-
CBS 322.94	230-350	?	36-42.5-47 x 19-21-23.5	2.02	?
A.R. 927	?	3	38-45.5-51 x 16-20-22.5	2.28	+
A.R. 9214	?	2	36-42-46 x 19-21.5-22.5	1.95	+
CBS 323.94	200-360	4	35-42.5-50 x 17.5-20-22	2.09	?
CBS 324.94	150-350	5	37-43-47.5 x 18-20-22.5	2.13	+
IMI 109554	?	2-3	35-50 x 15-22.5	?	?
CBS 176.37	285-400	3	36-41-45.5 x 15-18-19.5	2.28	+

Discussion:
The over 55-year-old (syn-)type culture CBS 176.37 of *M. thaumasium* (Fig. 54 a) revealed some interesting features: [p. 103]
   - Sporulation is not abundant and the typical luxurious branching of the conidiophore tip is lacking. Even in old cultures not more than two or three conidia per conidiophore are developed.
   - It produces microconidia, which have never been mentioned before for this species.
   - It spontaneously produces adhesive networks.
   - Conidiophore length and conidial measurements deviate from the original description (conidiophores 250-450 µm high, conidia 27-37-49 x 15-19.2-23 µm; Drechsler, 1937): conidiophores in a 12-day-old culture are mostly 350

µm long, not exceeding 400 µm. Conidia from 31- and 12-day-old cultures measure 35-42-53 x 16-19-22 µm and 36-41-45.5 x 15-18-19.5 µm, respectively. The average conidial length is thus significantly greater than given by Drechsler.

The conidial measurements of some strains studied intensively are listed in Table 8. In Fig. 54 the plasticity of the species is demonstrated. CBS 770.85 (received as *Geniculifera eudermata*) appears to fit well in the range of conidium length and width, even if the conidiophore shows geniculate tendencies.

Synonyms of *M. thaumasium*: Although no material of *M. cystosporum* could be studied (the type specimen only showed contaminants), *M. cystosporum* is regarded as a synonym of *M. thaumasium*. Though Cooke and Dickinson (1965) emphasized the two-celled conidia, this does not seem to be a reliable criterion for the separation of a species of the *M. thaumasium* complex, the more so as also three-celled conidia are produced in their isolate. The variability in conidial size and in the number of conidia per conidiophore is demonstrated by the ex-type culture of *M. thaumasium* and also is evident in Table 8.

The features of the ex-type culture of *M. globisporum*, ATCC 18498, partly differ from the original description, as can be seen from Table 9.

Table 9:
Conidiophore length and conidial size and percentage 1-septate, 2-septate and 3-septate conidia, in the original description and the type culture of *M. globisporum*.

Material	medium	conph.l.	conidial size (µm)	1-s	2-s	3-s	l:w
orig. descript	CMA	-300	37.5-38.8 x 17.5-22.5	56%	48%	rare	1.7
ATCC 18498	CMA:2	-400	31.5-38.8-42 x 16-18.4-20.5	-	70%	30%	2.1
ATCC 18498	MEA	?	35-38-43 x 16.5-18.5-21	-	90%	10%	2.05

The data given in Table 9 for the type culture reveal the variability of a strain, depending on the duration of culture and the medium. Cooke indicated as the main character for *M. globisporum* the one-septate and short conidia; but these could not be observed now. Using Cooke's (1967) 'key to species of *Monacrosporium* with adhesive networks', ATCC 18498 would run down to *M. cystosporum*. Presupposing that the most complex structure is taxonomically most significant, ATCC 18489 must be identified with one of the *Monacrosporium* species with three-septate conidia, the smallest three-septate conidia being found in *M. thaumasium*. Conidial morphology [p. 104] of the type culture (on two different media), is very similar to that of *M. thaumasium*, although conidia of the latter are slightly longer. Hence, *M. globisporum* R.C. Cooke is regarded as synonymous with *M. thaumasium*.

39. Monacrosporium turkmenicum (Soprunov) R.C. Cooke & C.H. Dickinson, *nom. inval.*

Dactylella turkmenica Soprunov - Kishchnye griby-gifomitseti i ikh primenenie v bor'be s patogenymi nematodami: 148. 1958 [nom. inval., Art. 37 ICBN] • *Monacrosporium turkmenicum* (Soprunov) R.C. Cooke & C.H. Dickinson - Trans. Br. mycol. Soc. **48**: 622. 1965 • *Golovinia turkmenica* (Soprunov) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 137. 1979.

Typification: not indicated. No illustration and no fresh material is available that would allow the validation of this species.

Characteristics (after Soprunov, 1958)**:** Conidiophores 400-600 µm high, bearing a single conidium on the tip, which may germinate and give rise to a second and a third conidium. Conidia almost spherical, 38-60 x 30-38 µm, inequidistantly three-septate. Chlamydospores not known. Trapping nematodes by means of constricting rings.

Discussion:
Soprunov described *M. turkmenicum* as being most similar to *M. eudermatum* what regards the conidial apparatus. The attention, however, has to be directed on species forming constricting rings. *M. aphrobrochum* and *M. coelobrochum* are four-septate, all other species forming three-septate conidia are much narrower. [p. 105]

10 Check-list of epithets used in *Dactylella, Geniculifera, Monacrosporium,* and related genera (excluding *Arthrobotrys*)

Recognized binomials are printed in **bold-face**. They reflect the newest or most appropriate combinations. All accepted species of *Monacrosporium* are described in this revision (unless there are particular reasons for their omission).
Species of *Dactylella* are illustrated when cultures were available.

acrochaeta (Dactylella) - see ***Monacrosporium acrochaetum***.

alaskana - *Dactylella alaskana* Matsush. - Icones microfungorum a Matsushima lectorum (Kobe): 53. 1975 • *Candelabrella alaskana* (Matsush.) Subram. - Kavaka **5**: 95. 1977 • **Arthrobotrys alaskana** (Matsush.) Oorschot - Stud. Mycol. **26**: 66. 1985.

Van Oorschot (1985) mentioned *A. alaskana* as being close to *A. pyriformis* (Juniper) S. Schenck, W.B. Kendr. & Pramer (predacious) and to *A. cylindrospora* (non-predacious, = *Dactylella cylindrospora* (R.C. Cooke) A. Rubner).

No type material was available. If *A. alaskana* turns out to be non-predacious, it should not be placed in *Arthrobotrys* any longer.

alba - *Menispora alba* Preuss - Sturm Deutschl. Fl., Pilze Bd. 6, Taf. 20. 1849; Linnaea **24**: 119. 1851 • *Dactylella alba* (Preuss) Sacc. - Sylloge Fungorum **4**: 194. 1886.

The type material was discovered in B but it does not allow an identification. Doubtful name.

ambrosium - *Monacrosporium ambrosium* Gadd & Loos - Trans. Br. mycol. Soc. **31**: 17. 1947 • **Fusarium ambrosium** (Gadd & Loos) Agnihotr. & Nirenberg - Stud. Mycol. **32**: 98. 1990 • *Dactylella ambrosia* (Gass & Loos) K.Q. Zhang, Xing Z. Liu & L. Cao - Mycosystema **7**: 112. 1995 ('1994') (with the younger synonyms *Fusarium bugnicourtii* Brayford • *Fusarium tumidum* var. *coeruleum* Bugn.).

anisomeres - **Dactylella anisomeres** Drechsler - Sydowia **15**: 359. 1962.

This species seems to be close to *D. spermatophaga* in conidiophore and conidium morphology and the ability to parasitize Oomycetes. It fits the concept of *Dactylella* well.

aphrobrocha *(Dactylella)* - see **Monacrosporium aphrobrochum**.

appendiculata - *Dactylella appendiculata* Anastasiou - see **Monacrosporium tentaculatum**.

appendiculata - *Golovinia appendiculata* Mekht. - Dokl. Akad. Nauk. Azerb. SSR. **10**: 90. 1976 • *Monacrosporium appendiculatum* (Mekht.) Xing-Z. Liu & K.-Q. Zhang - Mycol. Res. **98**: 864. 1994.

This species is of doubtful identity. Mekhtieva (1979) described the fungus in detail, indicating conidial measurements as 20–59 x 10–24 µm. The ranges of length and width are very unusual. Furthermore the (180) conidia measured by Mekhtieva seem to follow a three-phase [p. 106] distribution and there is no explanation of this phenomenon. The drawing shows three conidia of which one is only two-celled (probably immature), the second one is germinating and the third one, a three-septate conidium, strongly resembles *M. psychrophilum* in its ellipsoidal, rather than fusiform shape. No type available.

aquatica - *Pyricularia aquatica* Ingold [as '*Piricularia*'] - Trans. Br. mycol. Soc. **26**: 107. 1943 • *Dactylella aquatica* (Ingold) Ranzoni - Farlowia **4**: 359. 1953 • **Tumularia aquatica** (Ingold) Descals & Marvanová - Trans. Br. mycol. Soc. **89**: 506. 1987.

This genus is very distinct by dark mycelia and conidia (Descals and Marvanová 1987).

arcuata *(Dactylella)* - see **Monacrosporium arcuatum**

arnaudii - **Dactylella arnaudii** Yadav - Trans. Br. mycol. Soc. **43**: 603. 1960.

With branched conidiophores and hyaline, multiseptate, fusiform to rostrate conidia, this species resembles *D. oxyspora*. Like the latter, it is well placed in *Dactylella*.

The type-culture CBS 129.83 (IMI 77850) sporulates poorly.

asthenopaga *(Dactylella)* - see **Monacrosporium asthenopagum**.

atractoides - **Dactylella atractoides** Drechsler - Mycologia **35**: 357. 1943 • *Drechsleromyces atractoides* (Drechsler) Subram. - Kavaka **5**: 93. 1977.

Erection of a new genus for *D. atractoides* as proposed by Subramanian (1977) can hardly be justified if the generic concept of *Dactylella* also includes species with spindle-shaped conidia.

CBS 310.84 (from dead stem of *Cirsium arvense*, Zuid Flevoland, The Netherlands, W. Gams, March 1984) sporulates poorly. However, from Drechsler's drawing of *D. atractoides* (and the measurements given), the similarities with *D. oxyspora* are obvious.

beijingensis - **Dactylella beijingensis** Xing-Z. Liu, C.Y. Shen & W.-F. Qiu - Mycostema **5**: 113. 1992.

This species is not predacious as stated by the authors. Conidiophore length and conidial measurements resemble *Dactylella rhopalota* Drechsler. The latter, however, forms conidia of a more cylindrical shape (type specimen examined).

bembicodes *(Dactylella)* - see **Monacrosporium bembicodes**.

bogoriensis - *Genicularia bogoriensis* Rifai - Reinwardtia **7**: 367. 1968 • *Monacrosporium cystosporum* (Rifai, 1968).

This species is regarded as a synonym of **Monacrosporium thaumasium**.

brochopaga - *Dactylella brochopaga* Drechsler - Mycologia **29**: 517. 1937 • *Dactylaria brochopaga* (Drechsler) Drechsler - Mycologia **32**: 467. 1940 • *Dactylariopsis brochopaga* (Drechsler) Mekht. - Mikol. Fitopatol. **1**: 278. 1967

• **Arthrobotrys brochopaga** (Drechsler) S. Schenck, W.B. Kendr. & Pramer - Can. J. Bot. **55**: 982. 1977 • *Candelabrella brochopaga* (Drechsler) Subram. - Kavaka **5**: 95. 1977. [p. 107]

candidum *(Dactylium)* - see *Monacrosporium haptotylum*

Dactylium candidum (= *Dactylella candida*) is regarded as of doubtful identity (see p. 37). In order to avoid many name changes from *Monacrosporium* to *Dactylium*, it is proposed to reject the name (Gams and Rubner, 1995). *Dactylaria candida* sensu Drechsler has been synonymized with *M. haptotylum*.

capitulopaga - *Golovinia capitulopaga* (Drechsler) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 169. 1979 [*nom. inval.*, Art. 37 ICBN].
= *Dactylaria candida* auct., non (Nees) Sacc. 1886.
   This species is regarded as a synonym of *Monacrosporium haptotylum*.

carestianum - *Monacrosporium carestianum* Ferraris - Malpighia **18**: 500. 1904; Fl. Ital. crypt. 1. Fungi, Hyphales, p. 768. 1913.
   This is not a typical *Monacrosporium*. The original drawing shows relatively short conidiophores bearing almost cylindrical conidia constricted at the septum. Conidia are smaller than most of the *Monacrosporium* species described.

chinuanum - *Monacrosporium chinuanum* Xing-Z. Liu & K.-Q. Zhang - Mycol. Res. **98**: 863. 1994.
   From the original description and the type slide (So32-1), *M. chinuanum* is very similar to **M. haptotylum**. The authors distinguished this species from the latter by four- to five-septate conidia and branched conidiophores. No culture is available.
   In the 13 isolates of *M. haptotylum* studied (three- and) occasionally five-septate conidia were found besides the commonly four-septate conidia. Furthermore, the branched conidiophore tips described for *M. chinuanum* are not accepted as a distinctive character.

cionopaga - (*Dactylella*)- see *Monacrosporium gephyropagum*.

clavata - *Dactylella clavata* R.-H. Gao, M.-H. Sun & X.-Z. Liu - Mycosystema 56: 191. 1995.
   A non-nematophagous species with clavate, 3–6-septate conidia, 20–37–60 x 3–5 μm.

clavispora - *Dactylaria clavispora* R.C. Cooke - Trans. Br. mycol. Soc. **47**: 307. 1964 • *Genicularia clavispora* (R.C. Cooke) Rifai - Reinwardtia **7**: 367. 1968 • *Geniculifera*
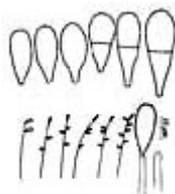

Fig. 55.
Arthrobotrys clavispora CBS 545.63 (ex-type culture) on CMA:2 (20 d, 30 d). Habit sketch of conidiophores, conidiophore tip, and conidia. [p. 108]

clavispora (R.C. Cooke) Rifai - Mycotaxon **2**: 216. 1975 • **Arthrobotrys clavispora** (R.C. Cooke) S. Schenck, W.B. Kendr. & Pramer - Can. J. Bot. **55**: 982. 1977 • *Nematophagus clavisporus* (R.C. Cooke) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 107. 1979. - Fig. 55.
   This species was originally described with conidiophores bearing 3–11 conidia on denticles on the tip and one- to two-septate conidia. Later it was transferred to *Geniculifera* because of a suggested geniculate conidiophore. Thus it would probably fit *Monacrosporium* in the present concept. The ex-type culture (CBS 545.63), however, rather points to *Arthrobotrys*: The conidia are mostly one-septate and often lack a septum, conidiophores are never seen to form denticles or geniculate branches. Conidia are much smaller than indicated by Cooke (1964), measuring 21.5–27(s.d. 3.6)–37 x 7.5–9.5(s.d. 1.2)–12.5 μm.
   Figure 54 shows somewhat puzzling conidiophores as they were seen under the dissecting microscope (with a magnification of 50 x), bearing several conidia scattered in the upper portions. In spite of several attempts, the conidiogenous loci could not be observed in microscopic slides.

coelobrocha *(Dactylella)* - see *Monacrosporium coelobrochum*.

constringens - *Arthrobotrys constringens* - Dowsett, J. Reid & Kalkat - Mycologia **76**: 559. 1984.
   This species is regarded as a synonym of *Geniculifera effusa* (= **Monacrosporium effusum**, p. 59) by Van Oorschot (1985).

copepodii *(Dactylella)* - see *Monacrosporium copepodii*.

coprophila - *Dactylella coprophila* Faurel & Schotter - Rev. Mycol. **30**: 157. 1965 [*nom. inval.*, Art. 37 ICBN].
   This species is regarded as a synonym of *Monacrosporium bembicodes*.

Fig. 56
Dactylella cylindrospora CBS 325.70 (ex-type culture) on CMA:2 (22 d). Habit sketch of conidiophores, conidiophore tips, and conidia. [p. 109]

cylindrospora - *Candelabrella cylindrospora* R.C. Cooke - Trans. Br. mycol. Soc. **53**: 477. 1969 (basionym) • *Arthrobotrys cylindrospora* (R.C. Cooke) S. Schenck, W.B. Kendr. & Pramer - Can. J. Bot. **55**: 982. 1977 • ***Dactylella cylindrospora*** (R.C. Cooke) A. Rubner, ***comb. nov.*** - Fig. 56.

    The species is non-nematophagous as already stated by Cooke (1969). The ex-type culture, CBS 325.70 (Fig. 56), exactly confirms Cooke's observations: conidiophore tips branched, non-arthrobotryoid, conidia hyaline, multiseptate, no trapping organs produced in the presence of *Turbatrix aceti*. According to the present generic concepts, *C. cylindrospora* does not belong to *Arthrobotrys* or *Monacrosporium* and is better placed in *Dactylella*.

cystosporium - *Trichothecium cystosporium* Dudd. - Trans. Br. mycol. Soc. **34**: 600. 1951 • *Arthrobotrys cystosporia* (Dudd.) Mekht. - Dokl. Akad. Nauk Azerb. SSR **20**: 70. 1964 • *Arthrobotrys cystosporia* (Dudd.) Sidorova, Gorlenko & Galepina - Bot. Zh. **49**: 1598. 1964 • *Genicularia cystosporia* (Dudd.) Rifai & R.C. Cooke - Trans. Br. mycol. Soc. **49**: 154. 1966 • *Geniculifera cystosporia* (Dudd.) Rifai - Mycotaxon **2**: 215. 1975 [non *Monacrosporium cystosporum* R.C. Cooke & C.H. Dickinson]

    Though no specimen is preserved, this species may be a later synonym of *Trichothecium inaequale* Massee & E.S. Salmon, see p. 111.

cystosporum - *Monacrosporium cystosporum* R.C. Cooke & C.H. Dickinson - Trans. Br. mycol. Soc. **48**: 623. 1965 • *Golovinia cystospora* (R.C. Cooke & C.H. Dickinson) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 146. 1979.

    This species is regarded as a synonym of ***Monacrosporium thaumasium***.

dasguptae - *Dactylaria dasguptae* S.K. Shome & U. Shome [as '*dasguptaii*'] - Mycopath. Mycol. appl. **30**: 216. 1966 [*nom. inval.*, Art 37 ICBN] • *Arthrobotrys dasguptae* (S.K. Shome & U. Shome) S. Schenck, W.B. Kendr. & Pramer - Can. J. Bot. **55**: 982. 1977 • *Dactylella dasguptae* (S.K. Shome & U. Shome) de Hoog & Oorschot - Stud. Mycol. **26**: 105. 1985.

    This species is regarded as a synonym of ***Monacrosporium leptosporum***.

doedycoides (*Dactylella*) - see ***Monacrosporium doedycoides***.

drechsleri (*Dactylella*) - see ***Monacrosporium drechsleri***.

effusa (*Dactylaria*) - *see **Monacrosporium effusum***.

elegans - ***Monacrosporium elegans***.

ellipsospora (*Menispora*) - see ***Monacrosporium ellipsosporum***.

eudermata (*Dactylaria*) - see ***Monacrosporium eudermatum***.

flagrans - *Trichothecium flagrans* Dudd. - Trans. Br. mycol. Soc. **32**: 287. 1949 • *Arthrobotrys flagrans* (Dudd.) Mekht. - Dokl. Akad. Nauk Azerb. SSR **20**: 70. 1964; combination also made by S. Schenck, W.B. Kendr. & Pramer - Can. J. Bot. **55**: 982. [p. 110] 1977 • ***Duddingtonia flagrans*** (Dudd.) R.C. Cooke - Trans. Br. mycol. Soc. **53**: 315. 1969 • *Arthrobotrys flagrans* (Dudd.)

    For the generic discussion see p. 39.

formosensis - *Dactylella formosensis* J. Sawada - Spec. Publ. Coll. Agric. Nat. Taiwan Univ. **8**: 189. 1959 [*nom. inval.*, Art. 36 ICBN].

According to the description, the species could be a *Cylindrocarpon* (W. Gams, pers. comm.).

fusariispora - *Kafiaddinia fusariispora* Mekht. [as '*fusarispora*'] - Mikol. Fitopatol. **12**: 8. 1978 • *Dactylella fusariispora* (Mekht.) K. Q. Zhang, Xing Z. Liu & L. Cao, Mycosystema **7**: 112. 1995 ('1994').

    The species is regarded as a synonym of ***Monacrosporium leptosporum***.

fusiforme - ***Monacrosporium fusiforme***.

gampsospora (*Dactylaria*) - see ***Monacrosporium gampsosporum***.

gephyropaga (*Dactylella*) - see ***Monacrosporium gephyropagum***.

globiformis - *Golovinia globiformis* Mekht. [as '(Drechsler) Mekht.'] - Khishchnye nematofagovye Griby-Gifomitsety: 157. 1979 [*nom. inval.*, Art. 37 ICBN].

= *Dactylella ellipsospora* auct., non (Preuss) Grove 1886.

    This species is regarded as a synonym of ***Monacrosporium ellipsosporum*** (Preuss) R.C. Cooke & Dickinson.

globisporum - *Monacrosporium globisporum* R.C. Cooke [as '*globosporum*'] - Trans. Br. mycol. Soc. **50**: 515. 1967 • *Golovinia globispora* (R.C. Cooke) Mekht. [as `*globospora*'] - Khishchnye nematofagovye Griby-Gifomitsety: 144. 1979.

    This species is regarded as a synonym of ***Monacrosporium thaumasium***.

gracilis - *Dactylaria gracilis* Dudd. - Trans. Br. mycol. Soc. **34**: 194. 1954 • *Arthrobotrys gracilis* (Dudd.) S. Schenck, W.B. Kendr. & Pramer - Can. J. Bot. **55**: 983. 1977 • *Dactylariopsis gracilis* (Dudd.) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 117. 1979.

In agreement with de Hoog and van Oorschot (1985), this species is regarded as a synonym of ***Arthrobotrys brochopaga*** (Drechsler) S. Schenck, W.B. Kendr. & Pramer.

haptospora - *Dactylaria haptospora* Drechsler - Mycologia **32**: 459. 1940 • ***Arthrobotrys haptospora*** (Drechsler) S. Schenck, W.B. Kendr. & Pramer - Can. J. Bot. **55**: 983. 1977 • *Kafiaddinia haptospora* (Drechsler) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 125. 1979 • *Dactyelella haptospora* (Drechsler) K. Q. Zhang, Xing Z. Liu & L. Cao, Mycosystema **7**: 112. 1995 ('1994').

haptotyla *(Dactylaria)* - see *Monacrosporium haptotylum*. [p. 111]

helminthodes- *Dactylella helminthodes* Drechsler - Mycologia **44**: 553. 1952.

This species parasitizes oospores of *Pythium* and zygospores of *Cochlonema megalosomum*. With its very short conidiophore (mostly about 10 µm high; Drechsler 1952), it is, like *D. stenomeces*, not a typical representative of the genus.

heptameres - ***Dactylella heptameres*** Drechsler - Mycologia **35**: 354. 1943.

There is some confusion about the nutritional behaviour of this species. Drechsler (1943, p. 352) wrote about a fungus occurring in a sample of leaf mould and producing small globose knobs and non-constricting rings. He then (l.c., p. 354) described the new fungus under the binomial *Dactylella heptameres*, but did not mention and draw these predacious organs.

Peach (1952) isolated a fungus from decaying leaf material, which she identified as *D. heptameres*. Her fungus was clearly non-predacious. The resulting culture (CBS 229.52, received as *D. heptameres*) could, however, be unambiguously reidentified as *M. gephyropagum*, producing the typical adhesive hyphal branches.

Thus it remains uncertain whether this species is in Drechsler's sense a member of the predacious series or not. Until a fungus with perfectly identical features is found, no transfer to *Monacrosporium* should be made.

heterospora *(Dactylella)* - see *Monacrosporium heterosporum*.

implexum - *Dactylium implexum* Berk. & Broome - Ann. Mag. Nat. Hist. Ser. 4, **11**: 345. 1873 • *Dactylella implexa* (Berk. & Broome) Sacc. - Syll. Fung. **4**: 194. 1886.

The original drawing shows *Dactylella*-like conidia, i. e. hyaline, phragmosporous, cylindrical, and 25.5–30.5 µm long. The conidiophores are thick and short (about 40–70 µm), and branched. Type material not seen.

inaequale - *Trichothecium inaequale* Massee & E.S. Salmon - Ann. Bot. **16**: 84. 1902 (basionym).
= *Geniculifera inaequalis* (Massee & E.S. Salmon) Subram. - Kavaka **5**: 96. 1977 [as 'inaequale'].
The two-celled conidia borne on geniculate conidiophores suggest a classification of this species in *Arthrobotrys*. Type material could not be located in NY, BM, and K; M did not answer a request. The morphology of the fungus as well as the original substratum suggest a member of the nematophagous series. The originally described conidial size matches that of *Arthrobotrys cystosporia* (Dudd.) Mekht., but because of the lack of a specimen, Rifai and Cooke (1966) preferred to retain the latter name.

indica - *Monacrosporiella indica* P.N. Chowdhry & N. Bahl [as 'indicum'] - Curr. Sci. **52**: 895. 1982 • ***Monacrosporium indicum*** (P.N. Chowdhry & N. Bahl) Xing-Z. Liu & K.-Q. Zhang - Mycol. Res. **98**: 865. 1994.

This species seems to be distinct from other species of *Arthrobotrys–Monacrosporium* complex by the branched conidiophores ('through nodes'). Conidia are borne singly on the tip of the conidiophore or in a thickened whirl; they are almost globose with a basal 'hilum', and zero- to two-septate. Thus, besides the atypical characters (nodes in the conidiophore and the conidial basal appendix), the species is intermediate between *Arthrobotrys* and *Monacrosporium*. [p. 112] Type material, indicated to be located in ITCC and HCIO, not seen. Its status remains doubtful.

inquisitor *(Dactylella)* - see *Monacrosporium inquisitor*.

Iridis- see *Monacrosporium iridis*.

leporinum - *Monacrosporium leporinum* Bubák - Annls. mycol. **4**: 120. 1906.

This species is of doubtful identity. Bubák described it insufficiently and did not draw it. The type specimen (BPI) consists of the natural substrate (rabbit dung), on which no hyphomycete can be observed. However, the conidiophore and conidium morphology speak for a species of *Monacrosporium*. Drechsler (1935, p. 495) regarded *M. leporinum* as identical with *Dactylella ellipsospora* (= ***Monacrosporium ellipsosporum***).

leptospora *(Dactylella)* - see *Monacrosporium leptosporum*.

lobata *(Dactylella)* - see *Monacrosporium lobatum*.

longiphorum - ***Monacrosporium longiphorum*** Xing-Z. Liu & B.-S. Lu - Mycostema **6**: 65. 1993.

The species could not yet be examined. From the original description, however, the fungus closely resembles *M. megalosporum* (Drechsler) Subram., differing from it by more slender conidia.

lysipaga (Dactylella) - see **Monacrosporium lysipagum**.

mammillata (Dactylella) - see **Monacrosporium mammillatum**.

megalobrocha - *Dactylella megalobrocha* Glockling - Mycol. Res. **98**: 847. 1994.
   The species could not be examined. No living culture has been preserved (M. W. Dick, pers. comm.) and no dried material could be obtained from IMI. The original description strongly suggests that *D. megalobrocha* is synonymous with **Monacrosporium bembicodes** (Drechsler) Subram. (p. 52).

megalospora (Dactylella) - see **Monacrosporium megalosporum**.

megasporum - *Monacrosporium megasporum* Boedijn - Recl Trav. bot. néerl. **26**: 428. 1929 • **Arthrobotrys megaspora** (Boedijn) de Hoog & Oorschot - Stud. Mycol. **26**: 80. 1985.

meliolicola - *Monacrosporium meliolicola* Cif. - Annls mycol. **36**: 244. 1938 • **Chionomyces meliolicola** (Cif.) Deighton & Pirozynski - Mycol. Pap. **128**: 75. 1972.
   Type material (from K; on *Meliola seyboensis* Ciferri, on leaves of *Ximenia americana* L.) revealed very broad conidiophore tips (about 7 μm), broad conidial bases and apical cells extending into a long tail. The mostly four-septate conidia measured 50–62 x 6–13 μm. Ciferri described the conidiophore as creeping to suberect, infrequently branched, 20–100 x 4–8 μm. He gave conidial measurements as 22–42 x 8–11 μm (with a very variable hyaline [p. 113] tail). The species does not belong to *Monacrosporium* and the classification in *Chionomyces* seems justified.

microaquatica - *Dactylella microaquatica* Tubaki - Bull. natn. Sci. Museum Tokyo **41**: 256. 1957 • **Monosporella microaquatica** (Tubaki) R.H. Petersen - Mycologia **54**: 120. 1962.
   This aquatic species is certainly not a *Dactylella*. Colonies are dark olive-brown, and the didymosporous conidia develop on short annellophores. The ex-type culture, CBS 216.59, does not sporulate on solid media under normal conditions.

microscaphoides - **Monacrosporium microscaphoides** Xing-Z. Liu & B.-S. Lu - Mycosystema **6**: 68. 1993.
   This species could not yet be examined. Judging from the original description, it is, however, better placed in the complex of *M. thaumasium*.

minuta - **Dactylella minuta** Grove - J. Bot. Lond. **22**: 199. 1884. - Fig. 57.
   The type specimen (located in K) consists of a piece of dead wood on which no *Dactylella* could be detected. A specimen of **Dactylella minuta** var. **fusiformis** (from stem of dead *Carduus* spec.), described by Grove (J. Bot. Lond. **24**: 129. 1886), neither revealed the fungus in question.
   Cultures of *D. minuta* are offered by CBS and MUCL [CBS 493.67, CBS 664.75, CBS 615.92 (= MUCL 11209), CBS 616.92 (= MUCL 11398), CBS 617.92 (= MUCL 22353)]. All these isolates were reidentified as **D. rhopalota**. They are all non-predacious. *D. minuta* (Fig. 57) should differ from *D. rhopalota* mainly by longer and especially wider conidia (60–70 x 14–15 μm).
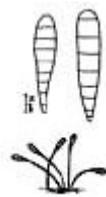

Fig. 57
Dactylella minuta, original illustration, redrawn from Grove (1884). Habit sketch of conidiophores and conidia.

moscovia - *Dactylariopsis moscovia* (Kond.) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 118. 1979 • *Dactylaria moscovia* Kondakova - Trudy Vsesoy. Inst. Zashch. Rast. **14**: 155. 1960 • *Dactylaria scaphoides* auct. non Peach (Kondakova, 1960).
   This species is regarded as a synonym of **Arthrobotrys scaphoides** (Peach) S. Schenck, W.B. Kendr. & Pramer (1977). [p. 114]

multiformis (Dactylella) - see **Monacrosporium multiforme**.

musiformis - **Arthrobotrys musiformis** Drechsler - Mycologia **29**: 481. 1937 • *Candelabrella musiformis* (Drechsler) Rifai & R.C. Cooke - Trans. Br. mycol. Soc. **49**: 163. 1966 • *Dactylella musiformis* (Drechsler) Matsush. - Microfungi of the Solomon Islands and Papua-New Guinea (Osaka): 22. 1971.
   The species is well-known to capture nematodes by means of two- and three-dimensional networks.

mutabile - **Monacrosporium mutabile**.

nematopaga - *Dactylaria nematopaga* Mekht. & Faisieva - Khishchnye nematofagovye Griby-Gifomitsety: 130. 1979 (basionym) • **Arthrobotrys nematopaga** (Mekht. & Faisieva) A. Rubner, **comb. nov.**
   Type material (located in Baku, Azerbaijan) was not requested. From the drawings the species is better placed in *Arthrobotrys* because of the arthrobotryoid conidiophore tip, although the conidia (35–90 x 10–15 μm) are

multiseptate. *A. nematopaga* shares many features with *A. polycephala* (Drechsler) Rifai.

obtrulloides - see ***Monacrosporium obtrulloides***.

oogena - *Dactylium oogenum* Mont. in Roum. - Arch. Méd. compar. **1**: 175. 1843 • *Dactylaria oogena* (Mont.) Sacc. - Syll. Fung. 4: 195. 1886.
    Fide de Hoog & van Oorschot (1985) this is possibly a ***Dactylella*** species.

ovatum - *Monacrosporium ovatum* Petch - Ann. R. Bot. Peradeniya **7**(4): 318. 1922.
    The species is of doubtful identity. The type material (from K) shows a Zygomycete on *Cocos nucifera*, but no *Monacrosporium*. Petch only described the fungus, but did not draw it.

oviparasitica - ***Dactylella oviparasitica*** Stirling & Mankau - Mycologia **70**: 777. 1978.
    This species is exclusively parasitic on nematode eggs and does not fit in *Monacrosporium*. An authentic culture (CBS 379.84) is sterile. Secondary isolates from the Netherlands (CBS 347.85, 348.85, and 349.85) seem to confirm its classification in *Dactylella* (Burghouts and Gams, 1989).

oxysporum - *Monacrosporium oxysporum* Sacc. & Marchal - Bull. Soc. R. Bot. Belgique **24**: 63. 1885 • ***Dactylella oxyspora*** (Sacc. & Marchal) Matsush. - Microfungi Solomon Isl. Papua-New Guinea: 22. 1971. - Fig. 58.
    The species is preferably placed in *Dactylella* because of the multiseptate conidia (up to 11 septa) without prominent middle cells. None of the isolates listed below was observed to develop trapping organs after induction with *Turbatrix aceti*.

Material examined:
CBS 257.70 (received as *D. rhombispora*), from agricultural soil, J.W. Veenbaas-Rijks. [p. 115]
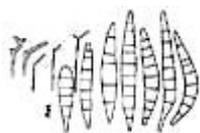

Fig. 58
Dactylella oxyspora, CBS 497.92 on CMA:2 (15 d). Habit sketch of conidiophores, conidiophore tips, and conidia.

CBS 280.70 (received as *D. rhombospora*), from old stem of *Angelica archangelica*, Germany.
CBS 157.89, from root of *Hordeum vulgare*, Netherlands, isol. M.Barth, det. W. Gams.
CBS 497.92 (= A.R. 922), from soil under bamboo, Stanford, California, USA, March 1991, coll. L. Smith (Fig. 58).
CBS 330.94 (= A.R. 932), from soil of a banana field, Puerto Naos, Tenerife, Dec. 1992, coll. G. Lysek.
A.R. 9322, from maize-field soil, Vilcabamba, Ecuador, Aug. 1993, coll. M.Hesse.
    Most isolates originate from soil of agricultural fields, probably a substratum favoured by the species.

papayae - *Dactylella papayae* J. Sawada - Spec. Publ. Coll. Agric. Nat. Taiwan Univ. **8**: 189. 1959 [*nom. inval.*, Art. 36 ICBN].
    The iconotype is not very distinctive and suggests a *Cylindrocarpon* (W. Gams, pers. comm.).

parvicollis *(Dactylella)* - see ***Monacrosporium parvicolle***.

passalopaga - ***Dactylella passalopaga*** Drechsler - J. Wash. Acad. Sci. **26**: 397. 1936.
    The species captures testaceous amoebae. The straight and relatively short conidiophores and the conidial apparatus suggest a relationship with species of *Dactylella*. No living culture is available.

paucispora - *Genicularia paucispora* R.C. Cooke, in Rifai & R.C. Cooke - Trans. Br. mycol. Soc. **49**: 157. 1966 • ***Arthrobotrys paucispora*** (R.C. Cooke) Jarow. - Acta mycol. **6**: 381. 1970 • *Geniculifera paucispora* (R.C. Cooke) Rifai - Mycotaxon **2**: 215. 1975. [p. 116]

perpasta - *Genicularia perpasta* R.C. Cooke in Rifai & R.C. Cooke - Trans. Br. mycol. Soc. **49**: 156. 1966 • ***Arthrobotrys perpasta*** (R.C. Cooke) Jarow. - Acta mycol. **6**: 381. 1970 • *Geniculifera perpasta* (R.C. Cooke) Rifai - Mycotaxon **2**: 216. 1975.

phymatopaga *(Dactylella)* - see ***Monacrosporium phymatopagum***.

polybrochum *(Trichothecium)* - see ***Monacrosporium polybrochum***.

polycephala - *Dactylaria polycephala* Drechsler - Mycologia **29**: 530. 1937 • ***Arthrobotrys polycephala*** (Drechsler) Rifai - Reinwardtia **7**: 371. 1968 • *Woroninula polycephala* (Drechsler) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 110. 1979.

polyctonum - *Trichothecium polyctonum* Drechsler - Mycologia **44**: 550. 1952 • ***Dactylella polyctona*** (Drechsler) K.Q. Zhang, Xing Z. Liu & L. Cao, Mycosystema **7**: 113. 1995 ('1994').
    A parasite of *Pythium* oospores with slender cylindrical 2-celled conidia borne on short, polyblastic conidiophores. No culture available.

psychrophila (Dactylaria) - see **Monacrosporium psychrophilum**.
Teleomorph: **Orbilia auricolor** (Bloxam ex Berk.) Sacc.

pulchra- *Dactylaria pulchra* Linder - Mycologia **26**: 438. 1934 • **Dactylella pulchra** (Linder) de Hoog & Oorschot - Stud. Mycol. **26**: 118. 1985.

The type specimen, flower pots made of tobacco stems as the natural substratum (in FH), did not reveal the fungus in question. It is probably a non-predacious species. Linder, in the original description, did not mention a nematode-trapping ability. Drechsler (1943) depicted a strain from greenhouse lettuce seedlings (*Lactuca sativa*), which he thought to be identical with *D. pulchra*, and which failed to attack any microscopic animals present in the Petri dish.

The conidiophore tips of *D. pulchra* are not typical of *Dactylella*: an irregular zig-zag-shaped rhachis with denticles, which bear the clavate, slightly spindle-shaped conidia.

pyriformis - *Dactylaria pyriformis* Juniper - Trans. Br. mycol. Soc. **37**: 437. 1954 • **Arthrobotrys pyriformis** (Juniper) S. Schenck, W.B. Kendr. & Pramer - Can. J. Bot. **55**: 984. 1977 • *Dactylariopsis pyriformis* (Juniper) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 119. 1979.

pyriformis - *Menispora pyriformis* Preuss - Linnea **24**: 120. 1851; Sturm, Deutschl. Fl. Pilze **6**: 95, Tab. 48. 1851 • *Dactylella pyriformis* (Preuss) Sacc. - Syll. Fung. **4**: 194. 1886.

This species is of doubtful identity as stated by Lindau (1905) because the number of conidial septa is not known. Original material from Preuss (in B) contained very small (about 6 x 2.5 μm), pyriform conidia without septa, and without any resemblance to species of *Monacrosporium*.

ramiformis (Dactylella) - see **Monacrosporium iridis**. [p. 117]

ramosa - **Dactylella ramosa** Matsush. - Microfungi Solomon Isl. Papua-New Guinea: 22. 1971.

Type material was not available. Matsushima (1971) did not indicate whether the species produces trapping organs. It seems correctly classified in *Dactylella*.

reticulata (Dactylella) - see **Monacrosporium reticulatum**.

rhombica - **Dactylella rhombica** Matsush. - Microfungi Solomon Isl., Papua-New-Guinea: 22. 1971.

No type material was available. As for *D. alaskana* and *D. ramosa*, Matsushima did not mention trapping organs. Otherwise the spindle-shaped conidia resemble those of species of *Monacrosporium*.

rhombispora - **Dactylella rhombispora** Grove [as 'rhombospora'] - J. Bot. Lond. **23**: 166. 1885.

This species is of doubtful identity. Grove did not indicate the height of the conidiophore nor the size of the conidia. The drawing shows rhomboid spores with seven septa, but their size cannot be determined. The type specimen (located at K) only consists of the natural substratum, on which the *Dactylella* in question could not be detected.

Drechsler (1935) found a non-predacious species of *Dactylella* which he identified as *D. rhombispora* without comparing it to *D. oxyspora*. All measurements given and the picture drawn by Drechsler do not conclusively prove the identity with Grove's *D. rhombispora*. The conspecifity of Drechsler's fungus with *D. oxyspora* seems more probable. The priority of the two taxa published in 1885 could not be settled.

rhopalota - **Dactylella rhopalota** Drechsler - Mycologia **35**: 357. 1943 • *Gangliophragma rhopalota* (Drechsler) Subram. - Kavaka **5**: 94. 1977. - Fig. 59.

With its relatively short (not exceeding 200 μm) and rarely branched conidiophores (as in CBS 615.92, a well-sporulating isolate - Fig. 59) and hyaline phragmoconidia (36-43.5–60 x 6–7.7–8.5 μm; with 3–10, mostly 7 septa), slightly clavate, rounded on the tip, *Dactylella rhopalota* is a good representative of the genus. None of the isolates tested formed trapping organs.
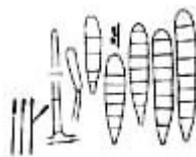

Fig. 59
Dactylella rhopalota CBS 615.92 on CMA:2 (15 d, 20 d). Habit sketch of conidiophores, conidiophore tips, and conidia. [p. 118]

Material examined:
CBS 493.67 (received as *D. minuta*), W. Gams, from wood of *Pinus sylvestris*, Netherlands.
CBS 475.70, J.C. Frankland, from living leaf of *Fraxinus excelsior*, U.K.
CBS 664.75 (received as *D. minuta*), from litter of *Juniperus communis*, Netherlands.
CBS 615.92 (= MUCL 11209) (received as *D. minuta*), from decaying wood, Netherlands.
CBS 616.92 (= MUCL 11398) (received as *D. minuta*), from needle of *Pinus* spec., Netherlands.
CBS 617.92 (= MUCL 22353) (received as *D. minuta*), Sweden.

There has been considerable confusion about the nutritional behaviour of the species. As mentioned for *D. minuta*, the isolates were described as capturing nematodes (CBS List of Cultures, 1994). Thakur and Zachariah (1989) expressed the feeling for their strain of *D. rhopalota* '... that under the right environmental conditions the same predatory activity [i. e. nematode egg parasitism as in *D. oviparasitica*] will be expressed.'

A teleomorph connection (see 5.1) has been discovered by Thakur and Zachariah (1989).

robustum - see ***Monacrosporium robustum***.

rutgeriense - *Monacrosporium rutgeriense* R.C. Cooke & Pramer [as '*rutgeriensis*'] - Phytopathology **58**: 544. 1968 [*nom. inval.*, Art. 37 ICBN].
   This species is regarded as a possible synonym of ***Monacrosporium eudermatum***.

salinum - see ***Monacrosporium salinum***.

sarcopodioides - *Acrothecium sarcopodioides* Harz - Bull. Soc. Imp. Nat. Moscou **44**: 123. 1871 • *Monacrosporium sarcopodioides* (Harz) Berl. & Vogl. - Addit. Syll. Fung.: 377. 1886.
   This species is of doubtful identity. Type material could not be located in GB, M did not answer a request. An isolate, CBS 239.33 (received as *M. sarcopodioides*, from Copenhagen, Denmark, det. F.H. van Beyma), is not a representative of *Monacrosporium*. According to W. Gams (pers. comm.), it is probably a *Cylindrocarpon* spec. (possibly the species known as *Trichothecium domesticum* Fr. : Fr.).

scaphoides - *Dactylaria scaphoides* Peach - Trans. Br. mycol. Soc. **35**: 19. 1952 • ***Arthrobotrys scaphoides*** (Peach) S. Schenck, W.B. Kendr. & Pramer - Can. J. Bot. **55**: 984. 1977 • *Woroninula scaphoides* (Peach) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 113. 1979 • *Monacrosporium scaphoides* (Peach) Xing-Z. Liu & K.-Q. Zhang - Mycol. Res. **98**: 865. 1994.
   The species is preferably placed in *Arthrobotrys* because of the arthrobotryoid conidiophore tip ('bearing a terminal group of large conidia, usually 5 to 12'; Peach, 1952).

sclerohypha - (*Dactylaria*)- see ***Monacrosporium haptotylum***.

sinense - ***Monacrosporium sinense*** Xing-Z. Liu & K.-Q. Zhang - Mycol. Res. **98**: 863. 1994.
   From the original description and the type slide (89192-1), it closely resembles *M. thaumasium*, and no significant deviations from the latter species could be detected. [p. 119]

spermatophaga - ***Dactylella spermatophaga*** Drechsler - Phytopathology **28**: 91. 1938.
   This species seems to be well placed in *Dactylella*. It has short conidiophores (commonly 35–75 µm high), slender conidia without prominent median cell, and a non-predacious, but mycoparasitic behaviour (on oospores and oogonia, mostly of *Pythium* and *Phytophthora*). CBS 255.76 (from oospores of *Phytophthora megasperma* var. *sojae*, Michigan, USA, B. Sneh) sporulates well.

sphaeroides - *Monacrosporium sphaeroides* Castaner - Am. Midl. Nat. **80**: 282. 1968 [*nom. inval.*, Art. 37 ICBN].
   No living culture is available. The original drawings and measurements suggest a synonymy with ***Monacrosporium eudermatum***.

stenobrochum (*Dactylella*) - see ***Monacrosporium stenobrochum***.

stenocrepis - ***Dactylella stenocrepis*** Drechsler - Sydowia **15**: 94. 1962.
   This oospore-parasitic species is very similar to *D. spermatophaga* and seems to fit well in *Dactylella*.

stenomeces- *Dactylella stenomeces* Drechsler - Phytopathology **53**: 1052. 1963.
   This parasite of *Pythium* oospores has unusually short conidiophores (mostly 10 to 50 µm; Drechsler, l.c.) and extremely long and slender conidia. It is not a typical representative of *Dactylella.*

strobilodes - ***Dactylella strobilodes*** Drechsler - Mycologia **42**: 371. 1950.
   This saprophytic species seems to fit the preliminary generic concept of *Dactylella*, though it morphologically also resembles *M. stenobrochum* (Drechsler, 1950).

submersa - *Piricularia submersa* Ingold - Trans. Br. mycol. Soc. **27**: 45-46. 1944 • ***Dactylella submersa*** (Ingold) S. Nilsson - Bot. Notiser **115**: 78. 1962.
   The habitat of this species (scum of fresh-water) is unusual for species of *Dactylella*. But the morphology of *D. submersa* does not contradict the present (preliminary) generic concept of *Dactylella*.

subtile - *Monacrosporium subtile* Oudem. - Ned. kruidk. Archf, Ser. **2**: 250. 1885.
   As for *M. elegans*, Oudemans (1885) did not mention any trapping organ for *M. subtile*. According to its morphology, it is unlikely that it would belong to the nematode-trapping fungi. The rather short conidiophores together with the cylindrical shape of conidia speak for a non-predacious *Dactylella*. No living culture is available. Type material could not be found in L.

synnematum - *Monacrosporium synnematum* Matsushima - Mats. Mycol. Mem. **8**: 26, Pl. 9, 10, 54. 1995.
   Conidiophore structure of this fungus suggests a species of *Arthrobotrys*, in spite of the mostly 4-celled conidia. It is close to *A. vermicola* (R.C. Cooke & Satchuth.) Rifai, which has slightly smaller conidia. [p. 120]

tedeschii - *Monacrosporium tedeschii* A. Agostini - Atti Ist. Bot. Univ. Pavia, Ser. **4**,4: 195. 1933.
   = ***Cylindrocarpon lichenicola*** (C. Massal.) D. Hawksw. - Bull. Br. Mus. (Nat. Hist.) **9**(1): 273. 1979.

An authentic isolate (CBS 279.34, from human skin, Mogadiscio, Somali Republic, leg. C. Tedeschi, det. A.Agostini) is sporulating and was reidentified as *Cylindrocarpon lichenicola* by W. Gams (pers. comm.).

tentaculatum - see *Monacrosporium tentaculatum*.

tenuis - ***Dactylella tenuis*** Drechsler - Mycologia **29**: 538. 1937.
    This non-predacious species seems to fit well in the preliminary generic concept of *Dactylella*. No living material is available.

thaumasia *(Dactylaria)* - see *Monacrosporium thaumasium*.

thaumasia var. ***longa*** - *Dactylaria thaumasia var. longa* S.M. Dixon - Friesia **5**: 406. 1956 [*nom. inval.*; Arts. 36, 37 ICBN].

turkmenica *(Dactylella)* - see *Monacrosporium turkmenicum* nom. inval.

tylopaga - *Dactylella tylopaga* Drechsler - Mycologia **27**: 220. 1935 • *Dactylina tylopaga* (Drechsler) Subram. - J. Indian bot. Soc. **42**: 297. 1963 • ***Lactydina tylopaga*** (Drechsler) Subram. - Kavaka **5**: 95. 1977.
    This amoebae-capturing fungus, with very short conidiophores (15–50 µm high; Drechsler, 1935) and two-celled conidia with an apical cellular appendage, does not seem to be closely related to other species of *Dactylella*. Subramanian (1963) proposed a new genus (*Dactylina*; *nom. illeg.*, Art. 53 ICBN) for solitary conidia with an appendage, and renamed it *Lactydina* in 1977. His concept seems to be justified because of the outstanding morphology of *D. tylopaga* and a probable basidiomycete affinity (Saikawa *et al.*, 1994).

vermicola - *Dactylaria vermicola* R.C. Cooke & Satchuth. - Trans. Br. mycol. Soc. **49**: 27. 1965 • ***Arthrobotrys vermicola*** (R.C. Cooke & Satchuth.) Rifai - Reinwardtia **7**: 371. 1968 • *Nematophagus vermicolus* (R.C. Cooke & Satchuth.) Mekht. - Khishchnye nematofagovye Griby-Gifomitsety: 105. 1979.

yunnanensis - *Dactylella yunnanensis* K. Q. Zhang, Xing Z. Liu & C. Lao, Mycosystema **7**: 113. 1995 ('1994').
    Description not yet available. The culture CBS 615.95 suggests identity with ***M. haptotylum.*** [p. 121]

11 Acknowledgements

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