A reevaluation of predatory orbiliaceous fungi. II. A new generic concept

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A new genus concept is proposed for predatory anamorphic *Orbiliaceae* in which the trapping device is the main morphological criterion for the delimitation of the genera. Molecular, ecological, physiological, biological, and further morphological features are taken into account as well. Following the groups identified by Hagedorn & Scholler (1999), these predatory fungi are divided into four genera: *Arthrobotrys* Corda forming adhesive networks, *Drechslerella* Subram. forming constricting rings, *Dactylellina* M. Morelet forming stalked adhesive knobs, and *Gamsylella* gen. nov. for species producing adhesive columns and unstalked knobs. Eighty-two species are accepted, for 51 of which new combinations are proposed.

Keywords: Nematophagous fungi, *Orbiliaceae*, *Arthrobotrys*, *Dactylellina*, *Drechslerella*, *Gamsylella* gen. nov., trapping devices, taxonomy.

Present generic and phylogenetic concepts for predatory orbiliaceous fungi and the taxonomic problems involved

Several specialized trapping devices are formed by anamorphs of predatory species of the *Orbiliaceae* (Ascomycota). Basic types are adhesive knobs, adhesive columns, adhesive networks, non-constricting, and constricting rings. They serve to trap and consume small animals, mainly nematodes. Since perfect states are unknown for the majority of nematophagous species, the morphology of the conidia (shape, number, and size of cells) and conidiophores (branching, modification of the apex) were preferentially used in delimiting genera. Most authors (e.g. Grove 1884, Drechsler 1937, Subramanian 1963, Rifai & Cooke 1966, Haard 1968, Jarowaja 1970, Mekhtieva 1979, van Oorschot 1985, Matsushima 1989, 1993) have based genera on differences in these structures. Besides the old and well known genera *Arthrobotrys* Corda, *Dactylaria* Sacc., *Dactylella* W. B. Grove, and *Monacrosporium* Oudem., a number of additional

genera have been proposed (for an overview see Rubner, 1996). Neither physiological or ecological features, nor the morphology of trapping devices, although being complex and morphologically stable, were considered taxonomically relevant. A few taxonomists used the latter as an additional criterion to delimit genera (Drechsler, e.g. 1937; Schenck & al., 1977; Rubner, 1996) or sections (Mekhtieva, 1967).

The inflation of generic concepts is due to the great number of species which do not fit in one or the other genus. The problems involved with the delimitation of the genera by conidial/conidiophore characters are indicated in a recent monograph of predatory hyphomycetes by Rubner (1996). The two accepted genera (*Arthrobotrys* and *Monacrosporium*) are distinguished by the formation or non-formation of conidiophore proliferations at the conidiophore apex, the presence or absence of an enlarged conidial middle cell, and the number of septa in the conidia. Like in earlier genus concepts, however, several species turn out to be intermediate and cannot be properly assigned to one or the other genus (e.g. *Arthrobotrys hertziana* M. Scholler & A. Rubner, recently described by Scholler & Rubner, 1999).

Using molecular methods like phylogenetic analyses of DNA sequences, taxonomic research of predatory fungi has made considerable progress in recent years. Persson & al. (1996) studied nematophagous species mainly belonging to the *Arthrobotrys oligospora* Fres. complex using RFLP analysis. Pfister (1997) compared rDNA sequences (ITS1, 5.8S, and ITS2) to infer a phylogenetic tree. His results indicate that trapping organs in general, and adhesive networks in particular, have evolved twice independently. In contrast, Liou & Tzean (1997), on the basis of the 5.8S rDNA sequences, proclaimed that nematophagous hyphomycetes are monophyletic. In a separate analysis using the more variable ITS regions (ITS1-ITS2), these authors found that the trapping devices are more important taxonomic characters than other morphological structures. They identified four monophyletic clades, each with a unique trapping device: adhesive networks (I), constricting rings (II), adhesive knobs (III), and adhesive columns (IV). *Monacrosporium phymatopagum* (Drechsler) Subram. with non-stalked knobs was used as an outgroup and was not included in any of the other groups. The authors suggested to place the four clades in separate genera.

A molecular study using 18S rDNA sequences was published by Ahrén & al. (1998). Their results resemble those of Liou & Tzean (1997), underlining the importance of trapping devices in delimiting genera. Ahrén & al. found, however, that non-predatory species (*Dactylella rhopalota* Drechsler, *D. oxyspora* (Sacc. & Marchal) Matsush.) form a separate group within the clade of nematode-trap-

ping species, indicating that the formation of trapping devices may have evolved at least twice independently or, alternatively, some species may have lost the ability to trap nematodes secondarily.

Further molecular data on predatory and related (anamorphic) ascomycetes were delivered by Hagedorn & Scholler (1999). The authors sequenced partial 18S rDNA, ITS1 region, 5.8S rDNA, and ITS2 region and combined their data with all available data from GenBank into a conspectus of the current knowledge of the phylogeny of predatory orbiliaceous hyphomycetes. Their analysis confirmed that trapping devices provide the most relevant morphological features for taxonomic purposes. In addition, a secondary loss of trapping structures as suggested by Ahrén & al. (1998) is shown to be unlikely. Hagedorn & Scholler (1999) agree with Liou & Tzean (1997) that genera should be delimited primarily according to their trapping device. Four major monophyletic groups of predatory taxa were identified in their analysis (using ITS1, 5.8S rDNA, and ITS2 sequences): taxa with constricting rings (I), taxa with adhesive networks (II), taxa with adhesive columns/unstalked knobs/proliferating unstalked knobs (III), and taxa with stalked adhesive knobs (IV). All groups have bootstrap support above 93%.

Taxonomic consequences: proposal for a new generic concept

A compilation of all available data on morphological and non-morphological characters for predatory orbiliaceous fungi (Tab. 1) reveals that many ecological, physiological, and biological characters do in fact correspond with the trapping device. Therefore, we believe that the framework of phylogenetic information is now stable enough to warrant a new generic concept for predatory orbiliaceous hyphomycetes.

A first genus comprises all species forming constricting rings (corresponding to group I in Hagedorn & Scholler, 1999). This group is exceptional in several aspects: (a) It is a sister group to all other predatory orbiliaceous fungi. (b) Its species form unusual trapping devices that lack adhesive material and which allow the fungus to actively fix and strangulate the nematode. (c) The species of this group have a characteristic physiological (weak cellulose decomposition) and another morphological (most species form conidia with a large middle cell) feature. The latter feature can also occur in groups II-IV, but not as frequently as in group I. *Monacrosporium bembicodes* (Drechsler) Subram. is included in this group although its position remains somewhat doubtful according to the molecular analysis of Hagedorn & Scholler (1999). We believe, however, that the presence of such a specialized trapping device is sufficient support to place this species within this genus. Pfister (1997) could es-

Tab. 1. – Ecological, physiological, biological, and morphological characters of four groups and two subgroups of predatory orbiliaceous fungi arranged according to their trapping organ. The numbers of the groups correspond to the numbers used in Hagedorn & Scholler (1999). ("+" feature present in more than 50% of the species, "(+)" feature in less than 50% of the species present, "–" feature never or very rarely present).

	Group I	**Group II**	**Group III**	**Group IV a**	**Group IV b**	**References**
	constricting ring	adhesive reticulate net	adhesive column	stalked adhesive knob alone	stalked adhesive knob and non-constricting ring	
Trapping devices detachable	+	–	–	+	+	Drechsler (1937), Duddington (1962), Barron (1975), Glockling & Dick (1994)
Colony radius more than 10 mm/3 d	–	+	–	–	–	Cooke (1963), Rubner (1996)
Saprotrophic activity	weak	strong	weak	weak	weak	Cooke (1963), Jansson (1982)
Spontaneous formation of traps	+	(+)	+	+	+	Cooke (1963), Jansson & Nordbring-Hertz (1979), Jansson (1982)
Attraction of the nematode *Panagrellus redivivus*	–	+	+	+	+	Jansson & Nordbring-Hertz (1979)
Cellulolytic activity	(+)	+	+	+	+	Rubner (1996)
Macroconidiophore tips with proliferations	–	(+)	–	(+)	(+)	original descriptions, van Oorschot (1985), Rubner (1996)

	Group I	Group II	Group III	Group IV a	Group IV b	References
	constricting ring	adhesive reticulate net	adhesive column	stalked adhesive knob alone	stalked adhesive knob and non-constricting ring	
Shape of macroconidia	mainly ellipsoidal, obovoidal, spindle- or top-shaped	mainly ellipsoidal, spindle-shaped, or obovoidal	mainly spindle-shaped	mainly cylindrical, ellipsoidal, spindle-shaped	mainly spindle-shaped	original descriptions, van Oorschot (1985), Rubner (1996)
Number of septa/ macroconidium	1–4	0–4(12)	3–5	1–7	3–5(15)	original descriptions, van Oorschot (1985), Rubner (1996)
Formation of microconidia	(+)	+	(+)	–	(+)	original descriptions, Barron (1979), van Oorschot (1985), Rubner (1996)
Formation of chlamydospores	(+)	+	–	–	–	original descriptions, Barron (1979), van Oorschot (1985), Rubner (1996)
Teleomorph genus	*Orbilia*	*Orbilia*	not known	not known	not known	Pfister (1994, 1997), Pfister & Liftik (1995), Webster & al. (1998), H. O. Baral (pers. com.)

tablish teleomorphs for two anamorphs from this group: *Orbilia spec.* for *Monacrosporium doedycoides* (Drechsler) R. C. Cooke & C. H. Dickinson and *Patinella tenebricosa* Svrček for *Monacrosporium polybrochum* (Drechsler) Subram. However, H. O. Baral (pers. comm.) also studied *P. tenebricosa* and recommends to transfer it to *Orbilia*. We therefore consider *Orbilia* to be the only teleomorph connection within this genus.

A second genus is recognized for species with mainly nematode-induced three-dimensional adhesive networks as trapping devices (group II in Hagedorn & Scholler, 1999). The species of this genus are further recognizable by fast mycelial growth, high saprotrophic activity, a high proportion of species possessing one-septate conidia, and by generally forming microconidia and chlamydospores. Several species are included in this group, which are characterized by other, simpler trapping structures. *Arthrobotrys musiformis* Drechsler sometimes forms two-dimensional networks. *A. gampsospora* (Drechsler) S. Schenck & al. and the strain SBUG-M No. 1264 (an undescribed species, see Hagedorn & Scholler, 1999) form loops which mostly do not fuse with the basal hyphae, giving rise to some distended filamentous branches. This type of trapping device is always formed spontaneously. The simplest structures are found in *A. botryospora* G. L. Barron and *A. "oligospora"* strain CBS 289.82: these species only produce simple adhesive loops which do not fuse with the basal hyphae, or just adhesive hyphae. Den Belder & al. (1994) reported only adhesive hyphae for the latter strain. We studied it and found simple loops as well (see Fig. 1). This proves that there is no species in group II that exclusively forms adhesive hyphae as are known from predatory species of the Zoopagaceae (Zygomycota). Strain CBS 289.82 is certainly different from *A. oligospora* as already shown by Persson & al. (1996). We consider all these simpler trapping devices secondary reductions of the basic type. The position of *A. anomala* G. L. Barron & D. E. Davidson seems to be doubtful, because this species produces three-dimensional networks as well as and adhesive columns (Barron & Davidson, 1972; they use the term "hyphal branch" for adhesive columns). This suggests that *A. anomala* is a missing link between groups II and group III. We think, however, that the columns of *A. anomala* are not homologous to adhesive columns formed by group III, but derived from adhesive networks and therefore prefer to place it in group II (see also discussion below).

The classification of species with unstalked adhesive knobs (e.g., *Monacrosporium lobatum* (Dudd.) A. Rubner), proliferating bending unstalked adhesive knobs (e. g., *M. arcuatum* Scheuer & J. Webster) A. Rubner), and straight multi-celled adhesive columns (e.g., *M. gephyropagum* (Drechsler) Subram.) in the next group is somewhat

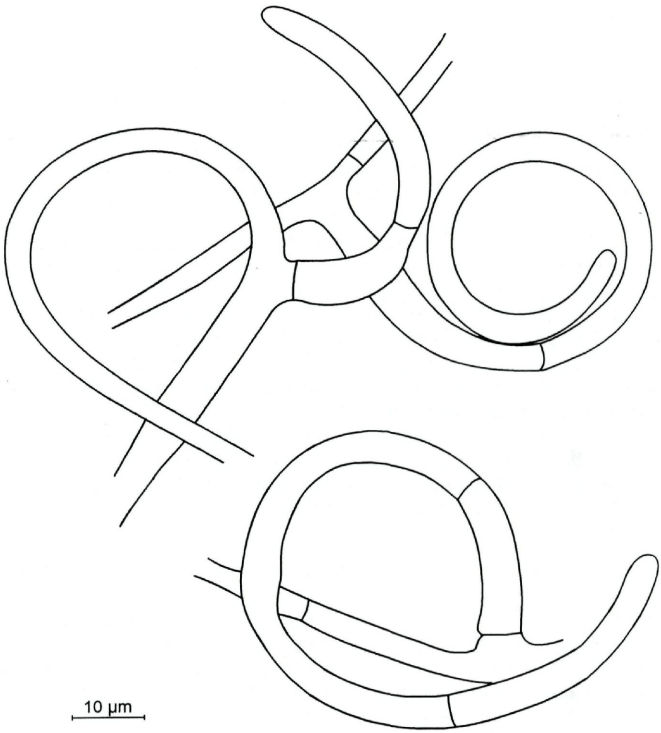

Fig. 1. – Adhesive loops formed by *Arthrobotrys "oligospora"* strain CBS 289.82.

controversial. One might propose a separate genus for the column formers, but we think that these three types of trapping organs are closely related and separate genera are not justified for the following reasons: First, in most species two different or even all three types of trapping devices are formed side by side (or one type develops from another one). Examples are *M. arcuatum*, producing unstalked knobs that can grow out to form columns or bended and branching proliferating knobs and *M. lobatum*, producing unstalked knobs that can grow out to form proliferating knobs. Second, it is difficult to distinguish proliferating knobs from adhesive columns. We call series of globose cells proliferating knobs, and series of more elongated

cells columns. It is possible that they are simply variations of the same structure.

Proliferating knobs and columns are distinguishable from simpler adhesive networks or branches of group II (*Arthrobotrys botryospora*, *A. anomala* etc.) by the globose cells that are constricted at the septa. In contrast, modified adhesive networks or branches always form cylindrical cells being not constricted at the septa. Therefore the poorly branching devices of *Monacrosporium arcuatum* have to be considered proliferating knobs and not sticky networks as reported by Scheuer & Webster (1990). The adhesive knob former *M. phymatopagum* may fall in either group III or IV (no bootstrap support for either, see Fig. 1 in Hagedorn & Scholler, 1999). We prefer to place this species in group III, because unstalked knobs clearly differ in shape from the spherical knobs of stalked knob formers in group IV. In addition, *M. phymatopagum* on rare occasions does form two-celled columns which are non-detachable (see illustrations in Drechsler, 1954: 778 and Rubner, 1996: 90). These are typical features of group III. Apart from the trapping device, group III is very similar to group IV (see Tab. 1). In the phylogram of Hagedorn & Scholler (1999), both groups form a common clade (as sister group of group II), albeit without bootstrap support.

Group IV is somewhat heterogeneous as well. It can be divided into two subgroups. Subgroup IVa forms stalked adhesive knobs, subgroup IVb additionally forms non-constricting rings. In the phylogram provided by Hagedorn & Scholler (1999) three of the four sequenced species of group IVb are placed in a monophyletic clade, whereas *Monacrosporium leptosporum* (Drechsler) A. Rubner strain CBS 560.92 is placed with high bootstrap support in an entirely different clade. As discussed by Hagedorn & Scholler (1999), this strain is possibly a misidentified member of group IVa because non-constricting rings were never observed in this isolate. If so, group IVb forms a monophyletic group that might be placed in a separate genus. Barron (1981: 177), however, speculated that species of group IVa may also produce non-constricting rings when suitably stimulated. Since all other characters are nearly identical in both groups (see Tab. 1), we decided to keep them in a single genus. Interestingly, there is a tendency in group IV to abandon nematodes and switch over to other hosts of animal origin. Whereas *Arthrobotrys entomopaga* Drechsler still attacks nematodes in addition to springtails (Drechsler, 1944), *A. ferox* Onofri & Tosi (springtails) and *Monacrosporium copepodii* (G. L. Barron) A. Rubner (copepodes) are apparently restricted to animal hosts other than nematodes. This feature is absent in all other groups.

Taxonomy and nomenclature

Four genera are recognized to accommodate the predatory orbiliaceous hyphomycetes. In agreement with, e.g., Schenck & al. (1977), de Hoog (1985), and Rubner (1996), we exclude nematophagous species from the genera *Dactylaria* Sacc. 1880 and *Dactylella* Grove 1884. The type species of these genera, *Dactylaria purpurella* (Sacc.) Sacc. and *Dactylella minuta* Grove, are non-predatory. The oldest available name for group I is *Drechslerella* Subram. 1963, for group II *Arthrobotrys* Corda 1839, and for group IV *Dactylaria sensu* Drechsler (*Dactylium* Nees 1817). However, rejection of the last-named, much confused genus and its type species, *D. candidum* Nees, has been proposed by Gams & Rubner (1997) and these proposals have been endorsed by the Committee for Fungi (W. Gams, pers. comm.). Alternatively, we select the genus *Dactylellina* Morelet 1968 for this group. For group III no genus name is available and we propose for it a new genus, *Gamsylella*.

In the following, amended descriptions of *Drechslerella*, *Arthrobotrys*, and *Dactylellina* are given and *Gamsylella* gen. nov. is described. In addition species lists of all genera are presented. Eighty-two species can be accepted, because either DNA sequences or trapping devices have been studied. For 51 of these species new combinations are proposed. The species concepts of de Hoog & van Oorschot (1985), van Oorschot (1985) and Rubner (1996) were accepted in most cases. In the species lists basionyms, facultative synonyms, and some important obligate synonyms are considered. For further synonyms see van Oorschot (1985) and Rubner (1996). A key for the species will be presented in a later publication. Fig. 2 shows a simplified phylogram based on ITS 1, 2, and 5.8S rDNA sequences analyzed by Hagedorn & Scholler (1999) with the new names of the sequenced species.

Drechslerella Subram. emend. M. Scholler, Hagedorn & A. Rubner

Type species: *Drechslerella acrochaeta* (Drechsler) Subram. – J. Ind. Bot. Soc. 42: 299 (1963).

≡ *Dactylella acrochaeta* Drechsler – Mycologia 44: 541 (1952).

= *Dactylariopsis* Mekht. (1967)

Type species: *D. brochopaga* (Drechsler) Mekht. – Mikol. Fitopatol. 1: 278 (1967).

≡ *Dactylaria brochopaga* Drechsler – Mycologia 29: 517 (1937).

= *Golovinia* Mekht. (1967)

Type species: *Golovinia bembicodes* (Drechsler) Mekht. – Mikol. Fitopatol. 1: 275 (1967).

≡ *Dactylella bembicodes* Drechsler – Mycologia 29: 491 (1937).

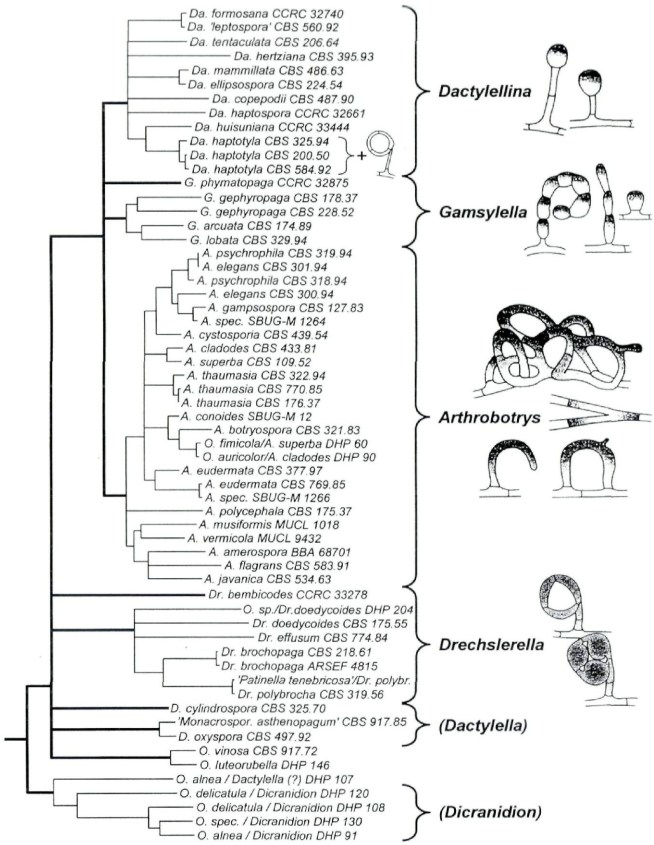

Fig. 2. – Phylogram based on the bootstrapped neighbor-joining analyses of Hagedorn & Scholler (1999); branches with bootstrap probabilities <75% are collapsed. See Hagedorn & Scholler (1999) for bootstrap values and outgroup rooting.

Mycelium slow-growing. – Hyphae septate, branching, hyaline. – Trapping nematodes by means of spontaneously formed stalked three-celled constricting rings; saprotrophic capacities weak. – Conidiophores simple or rarely branched, apex mainly simple without modifications, rarely with short denticles or with geniculate proliferations. – Conidia mainly formed singly at the tip of the

conidiophore, rarely in clusters. Conidia holoblastic, hyaline, one- to four-septate, mainly ellipsoidal, obovoidal, spindle-shaped, or top-shaped, rarely clavate, or cylindrical. – Microconidia and microconidiophores rarely observed. – Chlamydospores, when present, intercalary and in chains, thick-walled, spherical to ovoid, yellow pigmented. – Teleomorph, when known, belonging to the genus *Orbilia* Fr. (Helotiales).

Accepted *Drechslerella* species, including proposed new combinations

1. Dr. acrochaeta (Drechsler) Subram. – J. Ind. Bot. Soc. 42: 299 (1963).
   Basionym: *Dactylella acrochaeta* Drechsler – Mycologia 44: 541 (1952).
2. ***Dr. anchonia*** (Drechsler) comb. nov.
   Basionym: *Arthrobotrys anchonia* Drechsler – Mycologia 46: 762 (1954).
3. ***Dr. aphrobrocha*** (Drechsler) comb. nov.
   Basionym: *Dactylella aphrobrocha* Drechsler – Mycologia 42: 20 (1950).
4. ***Dr. bembicodes*** (Drechsler) comb. nov.
   Basionym: *Dactylella bembicodes* Drechsler – Mycologia 29: 491 (1937).
   = *Dactylella coprophila* Faurel & Schotter – Rev. Mycol. 30: 157 (1965) (invalid; Art. 37 ICBN).
   = *Dactylella megalobrocha* Glockling, in Glockling & Dick – Mycol. Res. 98: 847 (1994).
5. ***Dr. brochopaga*** (Drechsler) comb. nov.
   Basionym: *Dactylella brochopaga* Drechsler – Mycologia 29: 517 (1937).
6. ***Dr. coelobrocha*** (Drechsler) comb. nov.
   Basionym: *Dactylella coelobrocha* Drechsler – Mycologia 39: 17 (1947).
7. ***Dr. dactyloides*** (Drechsler) comb. nov.
   Basionym: *Arthrobotrys dactyloides* Drechsler – Mycologia 29: 486 (1937).
8. ***Dr. doedycoides*** (Drechsler) comb. nov.
   Basionym: *Dactylella doedycoides* Drechsler – Mycologia 32: 454 (1940).
9. ***Dr. effusa*** (Jarow.) comb. nov.
   Basionym: *Dactylaria effusa* Jarow. – Bull. Acad. Pol. Sci. Cl. 5: Ser. Sci. Biol. 16: 773 (1968).
   = *Arthrobotrys constringens* Dowsett, J. Reid & Kalkat – Mycologia 76: 559 (1984).

10. ***Dr. heterospora*** (Drechsler) comb. nov.
Basionym: *Dactylella heterospora* Drechsler – Mycologia 35: 347 (1943).
11. ***Dr. inquisitor*** (Jarow.) comb. nov.
Basionym: *Dactylella inquisitor* Jarow. – Acta Mycol. 7: 4 (1971).
12. ***Dr. polybrocha*** (Drechsler) comb. nov.
Basionym: *Trichothecium polybrochum* Drechsler – Mycologia 29: 536 (1937).
Teleomorph: *"Patinella tenebricosa"* Svrček –Česka Mykol. 31: 135 (1977); see Pfister (1997).
13. ***Dr. stenobrocha*** (Drechsler) comb. nov.
Basionym: *Dactylella stenobrocha* Drechsler – Mycologia 42: 10 (1950).

Arthrobotrys Corda *emend.* M. Scholler, Hagedorn & A. Rubner

Type species: *Arthrobotrys superba* Corda – Pracht-Flora Europ. Schimmelbildungen: 43 (1839).

= *Monacrosporium* Oudem. – Ned. Kruidk. Arch., Ser. 2,4: 250 (1885).
Lectotype species: *Monacrosporium elegans* Oudem. – Ned. Kruidk. Arch., Ser. 2,4: 250 (1885), designated by Clements & Shear (1931).

= *Didymozoophaga* Soprunov & Galiulina (1951) (invalid; Art. 36; illegit. Art. 52 ICBN)
Type species: *Didymozoophaga superba* (Corda) Soprunov & Galiulina – Mikrobiologiya 20: 494 (1951) (invalid; Art. 36 ICBN).
≡ *Arthrobotrys superba* Corda – Pracht-Flora Europ. Schimmelbildungen: 43 (1839).

= *Candelabrella* Rifai & R. C. Cooke (1966)
Type species: *Candelabrella javanica* Rifai & R. C. Cooke – Trans. Br. Mycol. Soc. 49: 160 (1966).

= *Duddingtonia* R. C. Cooke (1969)
Type species: *Duddingtonia flagrans* (Dudd.) R. C. Cooke – Trans. Br. Mycol. Soc. 53: 315 (1969).
Basionym: *Trichothecium flagrans* Dudd. – Trans. Br. Mycol. Soc. 32: 287 (1949).

= *Genicularia* Rifai & R. C. Cooke – Trans. Br. Mycol. Soc. 49: 153 [non *Genicularia* Rouss. ex Desv. 1808, non de Bary 1858] (nom. illeg.; Art. 53 ICBN; replaced by *Geniculifera*)
Type species: *Genicularia cystosporia* (Dudd.) Rifai & R. C. Cooke – Trans. Br. Mycol. Soc. 49: 154 (1966).
≡ *Trichothecium cystosporium* Dudd. – Trans. Br. Mycol. Soc. 34: 600 (1951).

= *Geniculifera* Rifai (1975)
Type species: *Geniculifera cystosporia* (Dudd.) Rifai – Mycotaxon 2: 215 (1975).
≡ *Trichothecium cystosporium* Dudd. – Trans. Br. Mycol. Soc. 34: 600 (1951).

= *Nematophagus* Mekht. (1975)
Type species: *Nematophagus azerbaidzhanicus* Mekht. – Mikol. Fitopatol. 9: 250 (1975).

= *Monacrosporiella* Subram. (1977)
Type species: *Monacrosporiella megalospora* (Drechsler) Subram. – Kavaka 7: 94 (1977).
≡ *Dactylella megalospora* Drechsler – Mycologia 46: 769 (1954).

= *Woroninula* Mekht. (1979)
Type species: *Woroninula polycephala* (Drechsler) Mekht. – Khishchnye nematofagovye Griby-Gifomitsety: 110 (1979).
≡ *Dactylaria polycephala* Drechsler – Mycologia 29: 530 (1937).

Mycelium fast-growing. – Hyphae septate, branching, hyaline. – Trapping nematodes by means of adhesive networks or modified devices, good saprotrophic capacities. Formation of traps induced by nematodes in most species. – Conidiophores simple or branched, apex mainly with short denticles or with geniculate, candelabrelloid, or percurrent proliferations, rarely simple without modifications. – Conidia either singly or in clusters at the tip of the conidiophore. Conidia holoblastic, hyaline, non-septate to multiseptate, mainly ellipsoidal, spindle-shaped or ovoidal, rarely clavate, cylindrical, pyriform, or turbinate. – Microconidia and microconidiophores frequently formed. – Chlamydospores, when present, intercalary or rarely terminal, singly or in chains, thick-walled, spherical to ovoid, yellow pigmented. – Teleomorph, when known, belonging to *Orbilia* Fr.

Accepted *Arthrobotrys* species, including proposed new combinations

1. *A. amerospora* S. Schenck, W. B. Kendr. & Pramer – Can. J. Bot. 55: 979 (1977).
2. *A. anomala* G. L. Barron & D. E. Davidson – Can. J. Bot. 50: 1773 (1972).
3. *A. apscheronika* Mekht. – Nov. Sist. Niz. Rast. 10: 174 (1973).
4. *A. azerbaidzhanica* (Mekht.) Oorschot – Stud. Mycol. 26: 70 (1985).
   ≡ *Nematophagus azerbaidzhanicus* Mekht. – Mikol. Fitopatol. 9: 250 (1975).
5. *A. botryospora* G. L. Barron – Can. J. Bot. 57: 1371 (1979).
6. *A. chazarica* Mekht. – Mycol. Res. 102: 683 (1998).
7. *A. cladodes* Drechsler var. *cladodes* – Mycologia 29: 463 (1937).
8. *A. cladodes* var. *macroides* Drechsler – Mycologia 36: 144 (1944). Teleomorph: *Orbilia auricolor* (Bloxam ex Berk.) Sacc. – Syll. Fung. 8: 625 (1889); see Pfister & Liftik (1995).
9. *A. clavispora* (R. C. Cooke) S. Schenck, W. B. Kendr. & Pramer – Can. J. Bot. 55: 982 (1977).
   ≡ *Dactylaria clavispora* R. C. Cooke – Trans. Br. Mycol. Soc. 47: 307 (1964).
10. *A. conoides* Drechsler – Mycologia 29: 476 (1937).
    = *Didymozoophaga dolioformis* Soprunov & Galiulina – Mikrobiologiya 20: 497 (1951) (invalid; Art. 36 ICBN).
    = *A. tortor* Jarow. – Acta Mycol. 4: 241 (1968).

11. *A. cystosporia* (Dudd.) Sidorova, Gorlenko & Nalepina – Bot. Zh. 49: 1598 (1964).
≡ *Trichothecium cystosporium* Dudd. – Trans. Br. Mycol. Soc. 34: 600 (1951).
12. *A. dendroides* Kuthub., Muid & Webster – Trans. Br. Mycol. Soc. 84: 564 (1985).
13. ***A. elegans*** (Oudem.) comb. nov.
Basionym: *Monacrosporium elegans* Oudem. – Ned. Kruidk. Arch., ser. 2, 4: 250 (1885) (for further synonyms see Rubner, 1996).
14. ***A. eudermata*** (Drechsler) comb. nov.
Basionym: *Dactylaria eudermata* Drechsler – Mycologia 42: 40 (1950).
15. *A. flagrans* (Dudd.) Sidorova, Gorlenko & Nalepina – Bot. Zh. 49: 1598 (1964).
Basionym: *Trichothecium flagrans* Dudd. – Trans. Br. Mycol. Soc. 53: 316 (1969).
≡ *Duddingtonia flagrans* (Dudd.) R. C. Cooke – Trans. Br. Mycol. Soc. 32: 287 (1969).
16. ***A. fusiformis*** (Drechsler) comb. nov.
Basionym: *Monacrosporium fusiforme* R. C. Cooke & C. H. Dickinson – Trans. Br. Mycol. Soc. 48: 628 (1965).
17. ***A. gampsospora*** (Drechsler) comb. nov.
Basionym: *Dactylaria gampsospora* Drechsler – Sydowia 15: 9 (1962).
≡ *Monacrosporium gampsosporum* (Drechsler) A. Rubner – Stud. Mycol. 36: 68 (1996).
18. ***A. guizhouensis*** (K.-Q. Zhang, Xing-Z. Liu & L. Cao) comb. nov.
Basionym: *Monacrosporium guizhouense* K.-Q. Zhang, Xing-Z. Liu & L. Cao – Mycol. Res. 100: 275 (1996).
19. *A. javanica* (Rifai & R. C. Cooke) Jarow. – Acta Mycol. 6: 373 (1970).
≡ *Candelabrella javanica* Rifai & R. C. Cooke – Trans. Br. Mycol. Soc. 49: 162 (1966).
20. ***A. indica*** (P. N. Chowdhry & N. Bahl) comb. nov.
Basionym: *Monacrosporiella indica* P. N. Chowdhry & N. Bahl [as "*indicum*"] – Curr. Sci. 52: 895 (1982).
21. ***A. iridis*** (Ts. Watan.) comb. nov.
Basionym: *Trinacrium iridis* Ts. Watan. – Mycologia 84: 794 (1992).
= *Dactylella ramiformis* Xing-Z. Liu & W.-F. Qiu – Mycol. Res. 97: 359 (1993).
22. ***A. longiphora*** (Xing-Z. Liu & B.-S. Lu) comb. nov.
Basionym: *Monacrosporium longiphorum* Xing-Z. Liu & B.-S. Lu – Mycosystema 6: 65 (1993).

23. ***A. megalospora*** (Drechsler) comb. nov.
Basionym: *Dactylella megalospora* Drechsler – Mycologia 46: 769 (1954).
24. ***A. microscaphoides*** (Xing-Z. Liu & B.-S. Lu) comb. nov.
Basionym: *Monacrosporium microscaphoides* Xing-Z. Liu & B.-S. Lu – Mycosystema 6: 68 (1993).
25. ***A. multiformis*** (Dowsett, J. Reid & Kalkat) comb. nov.
Basionym: *Dactylella multiformis* Dowsett, J. Reid & Kalkat – Mycologia 76: 563 (1984).
26. *A. musiformis* Drechsler – Mycologia 29: 481 (1937).
27. *A. obovata* K.-Q. Zhang & Xing-Z. Liu in K.-Q. Zhang, Xing-Z. Liu, L. Cao & R. H. Gao – Mycol. Res. 100: 529 (1996).
28. *A. oligospora* Fresen. var. *oligospora* – Beitr. Mykol. 1-2: 18 (1850).
= *A. rosea* Massee – J. R. Microsc. Soc., 2, 5: 758 (1885).
= *A. compacta* Mekht. – Nov. Sist. Niz. Rast. 10: 176 (1973). For further synonyms see van Oorschot (1985).
Teleomorph: *Orbilia auricolor* (Bloxam ex Berk.) Sacc. – Syll. Fung. 8: 625 (1889); see Pfister & Liftik (1995).
29. *A. oligospora* var. *microspora* (Soprunov) Oorschot – Stud. Mycol. 26: 84 (1985).
≡ *Trichothecium globosporum* Soprunov var. *microsporum* (Soprunov & Galiulina) ex Soprunov – Khishchnye Griby-Gifom.: 122 (1958).
= *A. microspora* (Soprunov) Mekht. – Dokl. Akad. Nauk Azerb. SSR 20: 70 (1964). For further synonyms see van Oorschot (1985).
30. *A. oligospora* var. *sarmatica* (Jarow.) Oorschot – Stud. Mykol. 26: 84 (1985).
≡ *A. "globospora"* (Soprunov) Sidorova, Gorlenko & Nalepina var. *sarmatica* Jarow. – Acta Mycol. 6: 371 (1970).
31. *A. oviformis* (Soprunov & Galiulina) ex Soprunov – Khishchnye Griby-Gifom.7731: 135 (1958).
≡ *Didymozoophaga oviformis* Soprunov & Galiulina – Mikrobiologiya 20: 497 (1951) (invalid; Art. 36 ICBN).
32. *A. paucispora* (R. C. Cooke) Jarow. – Acta Mycol. 6: 381 (1970).
Basionym: *Genicularia paucispora* R. C. Cooke, in Rifai & R. C. Cooke – Trans. Br. Mycol. Soc. 49: 157 (1966).
≡ *Geniculifera paucispora* (R. C. Cooke) Rifai – Mycotaxon 2: 215 (1975).
33. *A. perpasta* (R. C. Cooke) Jarow. – Acta Mycol. 6: 381 (1970).
≡ *Genicularia perpasta* R. C. Cooke, in Rifai & R. C. Cooke – Trans. Br. Mycol. Soc. 49: 156 (1966).
34. *A. polycephala* (Drechsler) Rifai – Reinwardtia 7: 371 (1968).
≡ *Dactylaria polycephala* Drechsler – Mycologia 29: 530 (1937).

35. ***A. psychrophila*** (Drechsler) comb. nov.
Basionym: *Dactylaria psychrophila* Drechsler – Mycologia 36: 161 (1944).
Teleomorph: *Orbilia auricolor* (Bloxam ex Berk.) Sacc. – Syll. Fung. 8: 625 (1889); see Rubner (1996).
36. *A. pyriformis* (Juniper) S. Schenck, W. B. Kendr. & Pramer – Can. J. Bot. 55: 984 (1977).
≡ *Dactylaria pyriformis* Juniper – Trans. Br. Mycol. Soc. 37: 437 (1954).
37. ***A. reticulata*** (Peach) comb. nov.
Basionym: *Dactylella reticulata* Peach – Trans. Br. Mycol. Soc. 33: 148 (1950).
38. *A. robusta* Dudd. – Trans. Br. Mycol. Soc. 34: 598 (1977).
39. ***A. salina*** (R. C. Cooke & C. H. Dickinson) comb. nov.
Basionym: *Monacrosporium salinum* R. C. Cooke & C. H. Dickinson – Trans. Br. Mycol. Soc. 48: 626 (1965).
40. *A. scaphoides* (Peach) S. Schenck, W. B. Kendr. & Pramer – Can. J. Bot. 55: 984 (1977).
≡ *Dactylaria scaphoides* Peach – Trans. Br. Mycol. Soc. 35: 19 (1952).
41. ***A. shahriari*** (Mekht.) comb. nov.
Basionym: *Candelabrella shahriari* Mekht. – Mycol. Res. 101: 334 (1997).
42. ***A. sinensis*** (Xing-Z. Liu & K.-Q. Zhang) comb. nov.
Basionym: *Monacrosporium sinense* Xing-Z. Liu & K.-Q. Zhang – Mycol. Res. 98: 863 (1994).
43. *A. superba* Corda – Pracht-Flora Europ. Schimmelbildungen: 43 (1839).
= *A. superba* var. *irregularis* Matr. – Rech. Dévelopg. Mucéd.: 73 (1892).
= *A. irregularis* (Matr.) Mekht. – Dokl. Akad. Nauk Azerb. SSR 27: 73 (1971).
= *Didymozoophaga kirghizica* Soprunov – Mikrobiologiya 20: 496 (1951) (invalid; Art. 36 ICBN).
= *A. drechsleri* Soprunov – Khishchnye Griby-Gifom.: 132 (1958) (invalid; Art. 36 ICBN).
Teleomorph: *Orbilia fimicola* Jeng & J. C. Krug – Mycologia 69: 832 (1889); see Pfister (1994).
44. ***A. tabrizica*** (Mekht.) comb. nov.
Basionym: *Nematophagus tabrizicus* Mekht. – Mycol. Res. 102: 683 (1998).
45. *A. thaumasia* (Drechsler) S. Schenck, W. B. Kendr. & Pramer – Can. J. Bot. 55: 984 (1977).
≡ *Dactylaria thaumasia* Drechsler – Mycologia 29: 522 (1937).
= *Monacrosporium cystosporum* R. C. Cooke & C. H. – Trans. Br. Mycol. Soc. 48: 623 (1965).

= *Monacrosporium globisporum* R. C. Cooke – Trans. Br. Mycol. Soc. 50: 515 (1967).

46. *A. vermicola* (R. C. Cooke & Satchuth.) Rifai – Reinwardtia 7: 371 (1968).
≡ *Dactylaria vermicola* R. C. Cooke & Satchuth. – Trans. Br. Mycol. Soc. 49: 27 (1966).

Doubtful and excluded species of *Arthrobotrys*

A. aggregata Mekht. – Mikol. Fitopatol. 6: 481 (1972) (invalid; Arts. 36, 37 ICBN).
The name was introduced by Mekhtieva (1972) to correct Drechsler's (1944) supposedly erroneous application of the name *A. arthrobotryoides* (Berl.) Lindau (see de Hoog & van Oorschot, 1985).

A. alaskana (Matsush.) van Oorschot – Stud. Mycol. 26: 66 (1985).
≡ *Dactylella alaskana* Matsush. – Ic. Microf. Matsushima lect.: 53 (1975).

According to van Oorschot (1985), this species resembles *A. pyriformis* and the non-nematophagous *A. cylindrospora* (R. C. Cooke) S. Schenck & al. (*Dactylella cylindrospora* (R. C. Cooke) A. Rubner). It is not known whether *A. alaskana* forms adhesive networks. We therefore prefer not to include it in *Arthrobotrys*.

A. anchonia Drechsler – Mycologia 46: 762 (1954).
See *Drechslerella anchonia*.

A. bacuensis Mekht. – Mikol. Fitopatol. 6: 481 (1972) (invalid; Arts. 36, 37 ICBN).
The name was listed in a table, without description or further reference (see van Oorschot, 1985).

A. brochopaga (Drechsler) S. Schenck, W. B. Kendr. & Pramer – Can. J. Bot. 55: 982 (1977).
See *Drechslerella brochopaga*.

A. anchonia Drechsler – Mycologia 46: 762 (1954).
See *Drechslerella anchonia*.

A. constringens Dowsett, J. Reid & Kalkat – Mycologia 76: 559 (1984).
See *Drechslerella effusa*.

A. cylindrospora (R. C. Cooke) S. Schenck, W. B. Kendr. & Pramer – Can. J. Bot. 55: 982 (1977).
≡ *Candelabrella cylindrospora* R. C. Cooke – Trans. Br. Mycol. Soc. 53: 477 (1969).
≡ *Dactylella cylindrospora* (R. C. Cooke) A. Rubner – Stud. Mycol. 39: 109 (1996).

This species is non-nematophagous. According to our generic concept, it belongs to the genus *Dactylella*.

A. dactyloides Drechsler – Mycologia 29: 486 (1937).
See *Drechslerella dactyloides*.

A. drechsleri Soprunov – Khishchnye Griby-Gifom.: 132 (1958) (invalid; Art. 36 ICBN).
See *A. superba*.

A. effusa (Jarow.) S. Schenck, W. B. Kendr. & Pramer – Can. J. Bot. 55: 982 (1977).
See *Drechslerella effusa*.

A. entomopaga Drechsler – Mycologia 36: 392 (1944).
See *Dactylellina entomopaga*.

A. ferox Onofri & Tosi – Mycotaxon 44: 446 (1992).
See *Dactylellina ferox*.

A. foliicola Matsush. – Ic. Microf. Matsushima lect.: 10 (1975).
The species is described as having pigmented conidiophores and very small conidia, which is untypical for *Arthrobotrys*. Matsushima (1975) did not mention any trapping devices, suggesting that it is no *Arthrobotrys* according to the authors concept. Molecular data (see Liou & Tzean, 1997) indicate that this species is not related to *Arthrobotrys*.

A. fruticulosa Mekht. – Mikol. Fitopatol. 6: 481 (1972) (invalid; Arts. 36, 37 ICBN).
The species was listed by Mekhtieva and presumably meant to replace *A. cladodes* var. *macroides* Drechsler sensu Soprunov but was not validly published (de Hoog & van Oorschot, 1985).

A. "globospora" (Soprunov) Sidorova, Gorlenko & Nalepina var. *microspora* Jarow. – Acta Mycol. 6: 371 (1970).
See *A. oligospora* var. *microspora*.

A. haptospora Drechsler – Mycologia 32: 459 (1940).
See *Dactylellina haptospora*.

A. irregularis (Matr.) Mekht. – Dokl. Akad. Nauk Azerb. SSR 27: 73 (1971).
See *A. superba*.

A. longa Mekht. – Nov. Sist. Niz. Rast. 10: 174 (1973).
According to de Hoog & van Oorschot (1985), the species is poorly described and no type material is available. Therefore, the species remains doubtful.

A. longiramulifera Matsush. – Matsushima Mycol. Memoirs 8: 14 (1995).

Matsushima (1995) did not mention any trapping devices. The species is considered doubtful until the nematode trapping capacity is tested.

A. megaspora (Boedijn) Oorschot – Stud. Mycol. 26: 80-81 (1985).
No trapping devices are known from this species (van Oorschot, 1985). The species is considered doubtful until the nematode trapping capacity is tested.

A. microspora (Soprunov) Mekht. – Dokl. Akad. Nauk Azerb. SSR 20: 70 (1964).
See *A. oligospora* var. *microspora*.

A. pauca J. S. McCulloch – Trans. Br. Mycol. Soc. 68: 176 (1977).
See *Dactylellina entomopaga*.

A. pravicovii (Soprunov & Galiulina) Mekht. – Dokl. Akad. Nauk. Azerb. S.S.R 20: 71 (1964).
≡ *Didymozoophaga pravicovii* Soprunov & Galiulina (as "*pravicovia*") – Mikrobiologiya 20: 496 (1951).
≡ *A. pravicovii* (Soprunov & Galiulina) Sidorova, Gorlenko & Nalepina – Bot. Zh. 49: 1598 (1964).
The type could not be traced by de Hoog & van Oorschot (1985). The authors studied material from BAKU which turned out to be *A. conoides*.

A. rosea Massee – J. R. Microsc. Soc., 2, 5: 758 (1885).
See *A. oligospora*.

A. "soprunovia" Mekht. – Mikol. Fitopatol. 6: 60 (1972).
This species was mentioned in Mekhtieva (1972), however, without reference.

A. stilbacea J. Meyer – Bull. Trimest. Soc. Mycol. Fr. 74: 246 (1958).
The species requires further investigation (de Hoog & van Oorschot, 1985).

A. straminicola Pidopl. – Mykrobiol. Zh. 9: 55 (1947).
No trapping devices are known from this species (van Oorschot, 1985).

A. strangulans Maupas, in Seurat. – Trav. Lab. Zool. Gén. Univ. Algér. (1920).
This species is doubtful (de Hoog & van Oorschot, 1985).

A. superba var. *irregularis* Matr. – Rech. Dévelopg. Mucéd.: 73 (1892).
See *A. superba*.

A. tortor Jarow. – Acta Mycol. 4: 241 (1968).
See *A. conoides*.

A. verrucosa Mekht. – Mikol. Fitopatol. 6: 481 (1972).
This species is mentioned in Mekhtieva (1972), however, no reference to a valid publication is given.

Gamsylella M. Scholler, Hagedorn & A. Rubner gen. nov.

Type species: *G. arcuata* (Scheuer & J. Webster) comb. nov.
Basionym: *Dactylella arcuata* Scheuer & J. Webster – Mycol. Res. 94: 718 (1990).
Typification: Holotype CBS H-4242, ex type culture CBS 174.89 (= IMI 333702).

Etymology. – In honour of Walter Gams, Austrian mycologist and expert on hyphomycetes, and to remind of the genus *Dactylella* to which the transferred species formerly belonged.

Fungi mitospori (Hyphomycetes). Mycelio tarde crescente, hyphis septatis, ramosis, hyalinis, saprotrophici vel praedatores; vermiculos nematoideos illaqueantes, cum ganglio viscoso vel columnis bi- ad multicellularibus: columnae ad septa constrictae, interdum laqueos formantes vel conjungentes. Formatio laqueorum spontanea. Macroconidiophora simplicia, interdum (ad apicem) ramosis, apicibus vulgo simplicibus, haud differentiatis. Conidia saepe solitaria, apicalia, holoblastica, hyalina, 3- ad 5-septata, fusiformia, raro clavata. Microconidia et microconidiophora raro formata. Chlamydosporae desunt. Teleomorphoses ignotae.

Mitosporic fungi (Hyphomycetes). – Mycelium slow-growing. – Hyphae septate, branching, hyaline. – Saprotrophic or predatory by trapping nematodes by means of unstalked non-detachable adhesive knobs or two- to multi-celled columns: columns constricted at the septa and sometimes forming loops or fusing with a neighboring column. Traps usually forming spontaneously. – Macroconidiophores mostly simple; branches, when present, often near the apex, apex mostly simple without modifications. – Conidia generally formed singly on the tip of the conidiophore, holoblastic, hyaline, three- to five-septate, mostly spindle-shaped, rarely clavate. – Microconidia and microconidiophores rarely formed. – Chlamydospores absent. – Teleomorph not known.

Species of *Gamsylella*, including proposed new combinations

1. ***G. arcuata*** (Scheuer & J. Webster) comb. nov.
   Basionym: *Dactylella arcuata* Scheuer & J. Webster – Mycol. Res. 94: 718 (1990).
2. ***G. gephyropaga*** (Drechsler) comb. nov.
   Basionym: *Dactylella gephyropaga* Drechsler – Mycologia 29: 512 (1937).
   = *Dactylella cionopaga* Drechsler – Mycologia 42: 30 (1950).
3. ***G. lobata*** (Dudd.) comb. nov.
   Basionym: *Dactylella lobata* Dudd. – Trans. Br. Mycol. Soc. 34: 489 (1951).

4. ***G. parvicollis*** (Drechsler) comb. nov.
   Basionym: *Dactylella parvicollis* Drechsler – Mycologia 15: 13 (1962) ("1961").
5. ***G. phymatopaga*** (Drechsler) comb. nov.
   Basionym: *Dactylella phymatopaga* Drechsler – Mycologia 46: 775 (1954).
6. ***G. robusta*** (R. S. McCulloch) comb. nov.
   Basionym: *Dactylella robusta* R. S. McCulloch. – Trans. Br. Mycol. Soc. 68: 177 (1977).

Dactylellina M. Morelet emend. M. Scholler, Hagedorn & A. Rubner

Type species: *Dactylellina leptospora* (Drechsler) M. Morelet – Bull. Soc. Sci. Nat. Archéol. Toulon Var 178: 6 (1968).
Basionym: *Dactylella leptospora* Drechsler – Mycologia 29: 507 (1937).

? = *Anulosporium* Sherb. (1933)
Type species: *Anulosporium nematopagum* Sherb. – Mycologia 25: 262 (1933).
The genus was erected for fungi with non-constricting rings, which were erroneously interpreted as spores. Since no conidia were described, the genus remains doubtful (Rubner, 1996: 36).

? = *Dactylium* Nees (1814) : Fries
Type species: *Dactylium candidum* Nees – Das System d. Pilze u. Schwämme: 58 (1817) : Fries, Syst. Mycol. 3: 382 (1832).
Generally considered a doubtful taxon, but interpreted by Drechsler (1937) in the sense of a predatory fungus then called *Dactylaria candida*, now synonymized with *Dactylellina haptotyla*. The names *Dactylium* and *Dactylaria candida* have been proposed for rejection (Gams & Rubner, 1997) and this rejection has been endorsed by the Committee for Fungi.

= *Dactylosporium* Mekht. (1967) [non Harz 1871] (nom. illeg., Art. 53 ICBN).
Type species: *Dactylosporium leptosporum* (Drechsler) Mekht. – Mikol. Fitopatol. 1: 278 (1967).
Basionym: *Dactylella leptospora* Drechsler – Mycologia 29: 507 (1937).

= *Kafiaddinia* Mekht. (1978)
Type species: *Kafiaddinia fusarispora* Mekht. – Mikol. Fitopatol. 12: 8 (1978).

= *Laridospora* Nawawi (1976)
Type species: *Laridospora appendiculata* (Anastasiou) Nawawi – Trans. Br. Mycol. Soc. 66: 344 (1976).
Basionym: *Dactylella appendiculata* Anastasiou – Pacif. Sci. 18: 202 (1964).

Mycelium slow-growing. – Hyphae septate, branching, hyaline. – Saprotrophic or predatory by trapping nematodes or other animals by means of stalked adhesive knobs, sometimes in combination with stalked three-celled non-constricting rings. Traps generally spontaneously formed. – Conidiophores mostly simple; branches, when present, often near the apex, apex mostly simple without modifications or sometimes with short denticles. – Conidia either formed singly or in clusters on the tip of the conidiophore, holoblastic, hyaline, 1–7(15)-septate, mostly cylindrical, ellipsoidal, fusiform or spindle-shaped, rarely clavate or obconical. – Micro-

conidia and microconidiophores very rarely formed. – Chlamydospores absent. – Teleomorph unknown.

Accepted *Dactylellina* species, including proposed new combinations

1. ***Da. appendiculata*** (Anastasiou) comb. nov.
   Basionym: *Dactylella appendiculata* Anastasiou – Pacif. Sci. 18: 202 (1964).
   ≡ *Monacrosporium tentaculatum* A. Rubner & W. Gams – Stud. Mycol. 39: 97 (1996).
2. ***Da. asthenopaga*** (Drechsler) comb. nov.
   Basionym: *Dactylella asthenopaga* Drechsler – Mycologia 29: 498 (1937).
3. ***Da. copepodii*** (G. L. Barron) comb. nov.
   Basionym: *Dactylella copepodii* G. L. Barron – Can. J. Bot. 68: 692 (1990).
4. ***Da. drechsleri*** (Tarjan) comb. nov.
   Basionym: *Dactylella drechsleri* Tarjan – Mycopath. Mycol. Appl. 14: 143 (1961).
5. ***Da. ellipsospora*** (Preuss) comb. nov.
   Basionym: *Menispora ellipsospora* Preuss, in Sturm – Deutschl. Fl. Abt. 3: H. 8: T. 47 (1851).
6. ***Da. entomopaga*** (Drechsler) comb. nov.
   Basionym: *Arthrobotrys entomopaga* Drechsler – Mycologia 36: 392 (1944).
   = ? *Arthrobotrys pauca* J. S. McCulloch – Trans. Br. Mycol. Soc. 68: 176 (1977).
7. ***Da. ferox*** (Onofri & Tosi) comb. nov.
   Basionym: *Arthrobotrys ferox* Onofri & Tosi – Mycotaxon 44: 446 (1992).
8. ***Da. formosana*** (J. Y. Liou, G. Y. Liou & Tzean) comb. nov.
   Basionym: *Dactylella formosana* J. Y. Liou, G. Y. Liou & Tzean – Mycol. Res. 99: 751 (1995).
9. ***Da. haptospora*** (Drechsler) comb. nov.
   Basionym: *Arthrobotrys haptospora* Drechsler – Mycologia 32: 459 (1940).
10. ***Da. haptotyla*** (Drechsler) comb. nov.
    Basionym: *Dactylaria haptotyla* Drechsler – Mycologia 42: 48 (1950).
    = ? *Dactylium candidum* Nees – Das System d. Pilze u. Schwämme: 58 (1817) – Fries, Syst. Mycol. 3: 44 (1829).
    = *Dactylaria candida* (Nees : Fr.) Sacc. – Syll. Fung. 4: 195 (1886).
    = *Dactylaria sclerohypha* Drechsler – Mycologia 42: 57 (1950).
    = *Monacrosporium chinuanum* Xing-Z. Liu & K.-Q. Zhang – Mycol. Res. 98: 863 (1994).

11. ***Da. hertziana*** (M. Scholler & A. Rubner) comb. nov.
Basionym: *Arthrobotrys hertziana* M. Scholler & A. Rubner – Mycol. Res. 103: 764–765 (1999).
12. ***Da. huisuniana*** (J. L. Chen, T. L. Huang & Tzean) comb. nov.-
Basionym: *Dactylella huisuniana* J. L. Chen, T. L. Huang & Tzean – Mycol. Res. 102: 1269 (1998).
13. *Da. leptospora* (Drechsler) M. Morelet – Bull. Soc. Sci. Nat. Archéol. Toulon Var 178: 6 (1968).
Basionym: *Dactylella leptospora* Drechsler – Mycologia 29: 507 (1939).
= *Dactylaria dasguptae* S. K. Shome & U. Shome – Mycopath. Mycol. Appl. 30: 216 (1966).
= *Kafiaddinia fusarispora* Mekht. – Mikol. Fitopatol. 12: 8 (1978).
14. ***Da. lysipaga*** (Drechsler) comb. nov.
Basionym: *Dactylella lysipaga* Drechsler – Mycologia 29: 503 (1937).
15. ***Da. mammillata*** (S. M. Dixon) comb. nov.
Basionym: *Dactylella mammillata* S. M. Dixon – Trans. Br. Mycol. Soc. 35: 144 (1952).
16. ***Da. mutabilis*** (R. C. Cooke) comb. nov.
Basionym: *Monacrosporium mutabile* R. C. Cooke – Trans. Br. Mycol. Soc. 53: 318 (1969).
17. ***Da. yunnanensis*** (K. Q. Zhang, Xing-Z. Liu & L. Cao) comb. nov.
Basionym: *Monacrosporium yunnanense* K. Q. Zhang, Xing-Z. Liu & L. Cao – Mycol. Res. 100: 275 (1996).

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