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TAXONOMIC STUDIES ON THE GENUS ARTHROBOTRYS CORDA [1]

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SUMMARY

Some 20 species of *Arthrobotrys* Corda have been listed in the literature. In this study, 8 have been studied from fresh material and the remainder from literary discussions. I have concluded that 12 are valid species, 7 doubtful and 1 a synonym. Two keys, one from pure and one from nematode-infested cultures, have been presented for the separation and identification of the valid species.

Arthrobotrys Corda is a genus of Hyphomycetes, presently containing 12 species, some of which are apparently distributed world-wide. While living mainly as saprophytes in soil, leaf duff, and decaying wood, *Arthrobotrys* species are also predators of nematodes and springtails (Collembola). Although the species of *Arthrobotrys* have received considerable attention in regard to their predaceous activity, few taxonomic studies have been made and thus a comprehensive treatment of the genus is greatly needed. It is hoped that the present study will serve to stimulate interest in these fungi.

The genus *Arthrobotrys* was described by Corda (**1839**) based on the type, *A. superba* Corda. The distinguishing characteristic was the formation of conidia on sterigmata in a whorled pattern at the tip and nodes of the conidiophore. Corda described the conidiophores as simple, erect, and septate, and the conidia as 2-celled with an apiculiform base.

Because of the similarity in conidiophore and conidia, *Trichothecium* Link. has often been confused with *Arthrobotrys*. Hoffman (**1854**) attempted to clarify this by noting that the whorled arrangement of conidia in *Arthrobotrys* is not present in *Trichothecium*. This was further discussed by Drechsler (**1937**). Coemans (**1863**) studied living material of *A. superba* and *A. longispora* Pr. and concluded that *A. superba* was the only valid species. However, he divided it into 3 varieties: 1) "superba," distinguished by its nodular conidiophore and

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its pyriform conidia; 2) "oligospora," also with pyriform conidia, but few nodes, and 3) an unnamed segment distinguished by its branched conidiophores. This was the first report of branching of the conidiophore. Coemans also referred to the species *A. recta* Pr. in his work but was unable to obtain material of it for study.

Matruchot (**1892**) reviewed the previous studies of the genus and concluded that *A. oligospora* Fres. and *A. superba* were distinct species. This was again emphasized by Drechsler (**1937**) who agreed with Matruchot that they differed in both conidium size and shape and in the presence of chlamydospores in *A. oligospora*. He also discovered that *A. superba* formed predaceous networks and verified Zopf's (**1888**) observation that *A. oligospora* did also.

With the work of Charles Drechsler (**1933**), the era of modern taxonomic studies was begun on the genus *Arthrobotrys* and other genera of predaceous fungi. He (**1933a**) isolated *A. oligospora* and 3 similar species from cultures of nematodes and diseased plant rootlets. Two of the species differed from *A. oligospora* only in conidial characteristics; however, the third was also different in that it formed a single terminal head of conidia born on extremely long sterigmata.

Drechsler (**1941**) reviewed much of the previous work and briefly discussed the history of the genus and marked its important events.

Dollfus (**1946**) also contributed a fairly complete review of the taxonomy of predaceous fungi and their relationship to nematodes. He collected much of the previous work and compiled a complete list of references.

At this time, Duddington began to work on predaceous fungi in Great Britain. The first of his articles (**1950**) was taken from his lecture at the Quekett Microscopal Institute and was an outline on the predaceous fungi, including known facts about the Zoopagaceae, the Hyphomycetes, and other predaceous fungi.

A third taxonomic review, presented by Soprunov (**1958**), included 4 new species isolated in Russia.

Cooke and Godfrey (**1964**) presented a key to common species of several genera of predaceous fungi based on a review of the literature. It includes characteristics from both pure and nematode-infested cultures.

The most recent taxonomic work is that of Rifai and Cooke (**1966**). In this work, they compare *Trichothecium* Link., *Geniculariа* Rifai & Cooke, *Candelabrella* Rifai & Cooke, and *Arthrobotrys* Corda.

METHODS AND MATERIALS

A study was made of 37 isolates of *Arthrobotrys*. Six were obtained from U. S. Army Natick Laboratories Culture Collection and 5 from Centraal-bureau voor Schimmelcultures, Baarn, Holland. The remaining 26 were isolated by the author from soil and decaying organic matter.

Isolations were made by placing small amounts of soil or decaying organic material on plates of Difco maizemeal agar (17 g/liter) and incubating them at 25 C. Examination of the plates was made at weekly intervals over a 3 month period. When sporulation began, conidia from a single conidiophore were transferred to maizemeal agar on which the isolates were maintained in pure culture.

Studies were made on both pure and nematode-infested cultures. In pure culture, all studies were made using isolates grown on Difco maizemeal agar. All measurements of conidia were made from mounts in lactophenol-cotton blue or Phloxine with 1% KOH within 10 min after preparation of the slide. Longer exposure to these mounting media often caused shrinkage in spore size.

Nematode-infested cultures were prepared by establishing cultures of miscellaneous soil nematodes on plates of maizemeal agar which had previously been inoculated with various genera of soil bacteria and then inoculating the culture with blocks of agar containing mycelium cut from pure culture plates.

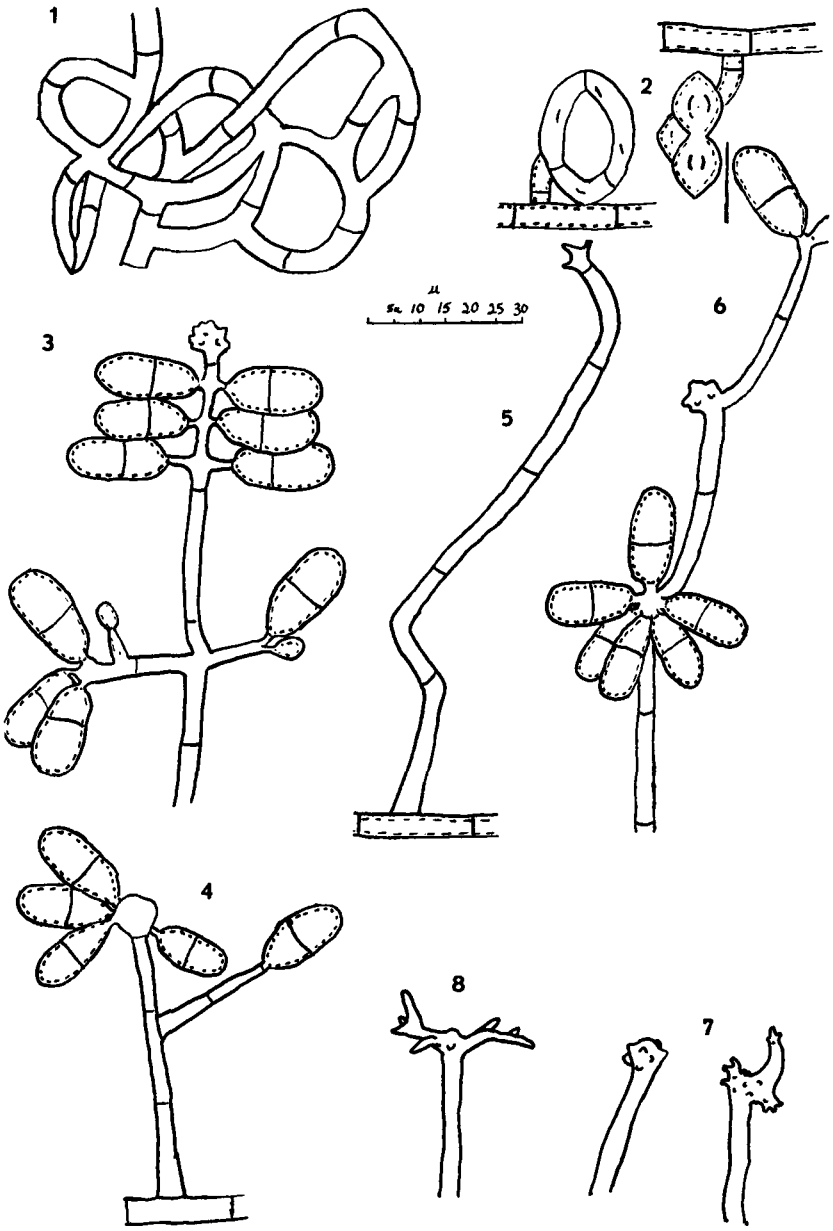
TAXONOMIC FEATURES

The following results are based on a study of 8 species of *Arthrobotrys* in pure and nematode-infested cultures.

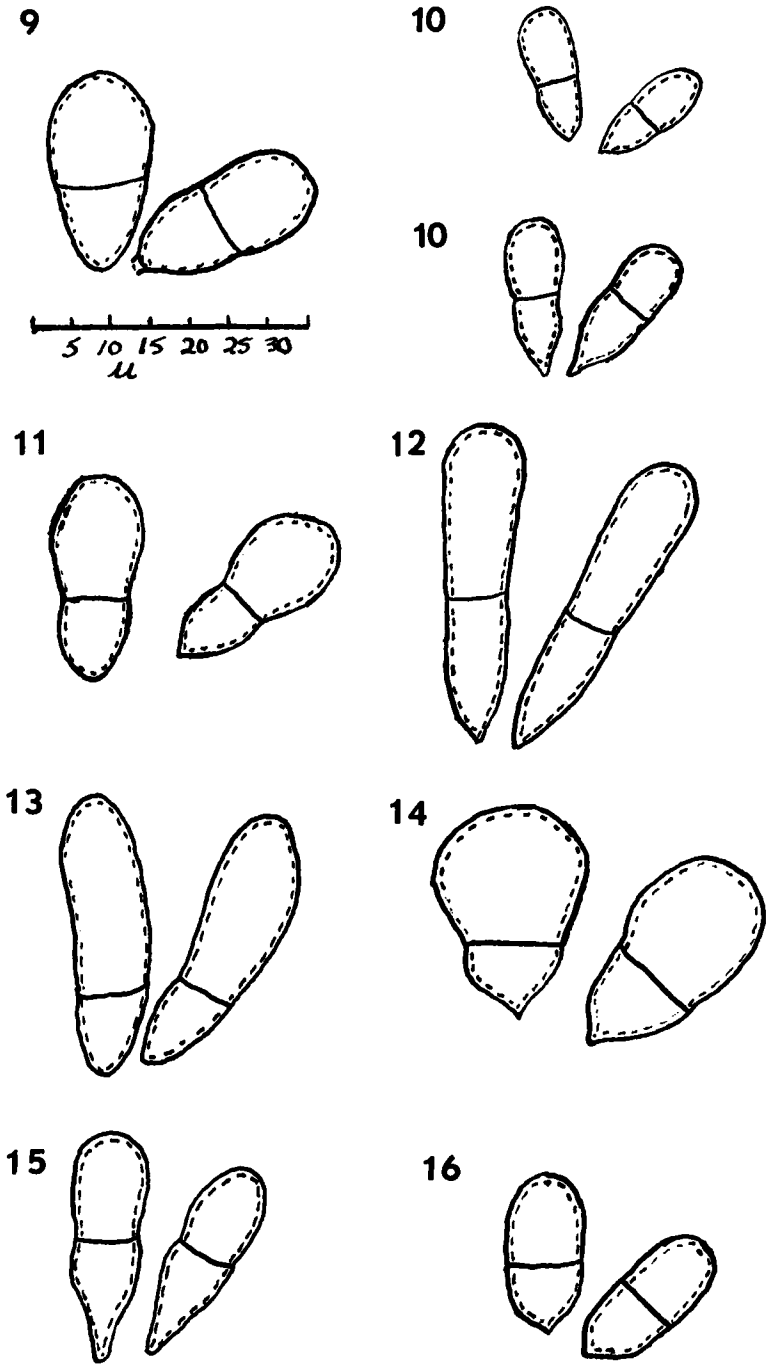
Mycelium.—The mycelium is hyaline and septate. It is composed of hyphae 2–7 μ wide which frequently fuse to form coils which give rise to conidiophores.

Predaceous organs.—In nematode-infested cultures and occasionally in pure culture the mycelium forms predaceous organs by modified hyphal branching. The predaceous organs are of three general types, networks, constricting rings, and aerial sticky knobs.

Networks are of two types: 3-dimensional which are composed of many 3- to 5-celled loops fused in all directions thereby allowing part of the network to lie prostrate on the substratum and part to rise above the substratum (FIG. 1), and 2-dimensional which may be composed of either a single 4-celled, adhesive, horseshoe-shaped loop or several such loops fused so that the entire network lies in a single plane, usually perpendicular to the substratum. Both types capture nematodes by adhesion and entanglement.



FIGS. 1–8. Species of *Arthrobotrys*. 1. Networks, *A. conoides*. 2. Constricting rings, *A. dactyloides*. 3, 4. Branched conidiophores, *A. arthrobotryoides*. 5. Unbranched conidiophore, *A. dactyloides*. 6. Nodular conidiophore, *A. superba*. 7. Wartlike sterigmata, *A. arthrobotryoides*. 8. Branched sterigmata, *A. musiformis*.



FIGS. 9–16.

The constricting ring (FIG. 2) is composed of two parts, a ring and a stalk. The ring is made of 3 arcuate cells. The first and third cells are fused to the curved stalk which holds the ring perpendicular to the substratum. The stalk consists of a short basal cell and a slightly longer distal cell. Several rings form on a single hypha and lie in or on the substratum. As a nematode attempts to move through a ring, it stimulates the three ring cells to inflate and thus hold the nematode fast. When one ring is stimulated to close, all rings on the same hypha may close.

Aerial predaceous organs are known in only one species, *A. entomopaga* Drechs., which was not obtainable for study.

Once a nematode or springtail is captured by any of the various trapping devices, the predaceous organ produces a hypha that penetrates the victim's integument and produces a swollen vesicle on the inside. This vesicle in turn produces several assimilative hyphae that grow throughout the victim absorbing its contents and eventually leaving only the integument.

Conidiophores.—The conidiophores in the genus are hyaline, septate, erect, single, free, and distinct. They range from 20–500 μ in length and from 3.5–9 μ in width at the base, tapering gradually toward the tip. They may originate from either prostrate or aerial mycelium and may be branched (FIGS. 3, 4) or unbranched (FIG. 5).

All species have terminal capitate heads of conidia. However, in some species, the conidiophore can elongate to form 3–30 additional heads or nodes of conidia (FIG. 6). The ability to branch and produce nodes is often lost in nematode-infested cultures.

The spore bearing portion of the conidiophore may be swollen and bear short wartlike sterigmata (FIG. 7) or it may be nonswollen with longer branching sterigmata (FIG. 8). Both types occur in a whorled arrangement, and intergradation between the two types occurs.

Conidia.—Conidia are hyaline and uniseptate with usually a broad distal and an apiculate proximal cell. Each conidium is borne singly on a sterigma. The size and shape of the conidia vary with the species (FIGS. 9–16). They may be ovoid, elongate ovoid, obovoid, elongate obovoid or ellipsoid. Some are slightly curved while others are perceptibly constricted at the septum. In size, they are 10–50 $\mu \times$ 4.5–16 μ.

FIGS. 9–16. Conidia of species of *Arthrobotrys*. 9. *A. arthrobotryoides*. 10a. *A. cladodes* var. *cladodes*. 10b. *A. cladodes* var. *macroides*. 11. *A. conoides*. 12. *A. dactyloides*. 13. *A. musiformis*. 14. *A. oligospora*. 15. *A. robusta*. 16. *A. superba*.

Chlamydospores.—Chlamydospores are found in some species, but occur only in old cultures. They are yellowish and spherical to oblong. They may occur singly or in chains and may be intercalary in prostrate hyphae or terminal at the ends of prostrate hyphal branches.

Pure culture vs. nematode-infested colonies.—Colonies appearing on nematode-infested plates are composed almost entirely, if not completely, of prostrate mycelium which gives rise to a sparse development of conidiophores. The conidiophores often do not branch or develop nodes to the extent that they do in pure culture. Predaceous organs often develop only in nematode-infested culture. In contrast, colonies in pure culture are composed of both aerial and prostrate mycelium, both of which may give rise to normal conidiophores.

Phylogeny.—The 12 species of *Arthrobotrys* here recognized as being valid can be divided into 4 distinct groups according to conidiophore types when grown in pure culture on maizemeal agar. These

TABLE I

MAJOR GROUPS WITHIN THE GENUS ARTHROBOTRYS

Group	Characteristics		Species
	Conidiophores	Predaceous organs	
I	Branched, non-nodular	3-D networks	*A. cladodes* *A. robusta*
II	Branched, nodular	3-D networks	*A. arthrobotryoides* *A. dolioformis* *A. oviformis*
IIIa	Unbranched, non-nodular	2-D networks	*A. musiformis*
IIIb	Unbranched, non-nodular	Constricting rings	*A. anchonia* *A. dactyloides*
IVa	Unbranched, nodular	3-D networks	*A. conoides* *A. oligospora* *A. superba*
IVb	Unbranched, nodular	Aerial predaceous organs	*A. entomopaga*

groups (TABLE 1) indicate some interesting trends of development in conidiophore formation and correspondingly in the type of predaceous organs developed in nematode-infested cultures.

The simplest forms are found in those species listed in Group I. These species have conidiophores that are little more than erect or suberect vegetative hyphae which have differentiated to the point that each branch bears a terminal head of conidia. The branched conidiophores develop either a swollen conidiophore tip with "wartlike" sterigmata or a non-swollen tip with short "branchlike" sterigmata. All members within this group form predaceous networks in nematode-infested cultures.

Group II is similar to Group I in having branched conidiophores and network-like predaceous organs. The conidiophores also have swollen tips and bear their conidia on short "wartlike" sterigmata. However, they differ in having a nodular development of the conidiophores which appears to be a step away from the vegetative growth habit.

Group III has unbranched, non-nodular conidiophores with non-swollen tips and short "branchlike" sterigmata. One of the species included in this group has developed predaceous organs referred to as 2-dimensional networks. These appear to be somewhat intermediate between the 3-dimensional networks and the 3-celled constricting rings characteristic of the other two species of this group.

In Group IV, the conidiophores are nodular and unbranched with swollen tips which bear short "wartlike" or "branchlike" sterigmata. All but one species in this group form predaceous networks. The other one, *A. entomopaga,* has networks that have undergone considerable specialization and function in the capture of springtails rather than nematodes. These networks form specialized aerial organs at the juncture of fused hyphae. These organs consist of two elongated cells, the distal of which secretes a sticky material that entraps by adhesion.

ARTHROBOTRYS Corda, Pract-Flora Europaeishcher Schimmelbildungen. 1839.

Syn: *Didymozoophaga* Soprunov & Galiulina, Mikrobiologiya **20**: 489–499. 1951.

Colony in pure culture on maizemeal agar white to pale rose or yellow, spreading rapidly in a circular or irregular circular pattern; mycelium septate, hyaline, prostrate or aerial, often fusing with itself; conidiophores hyaline, septate, erect, single, branched or unbranched, free and distinct bearing terminal heads of conidia on sterigmata in a whorled pattern, sometimes elongating after first head to form 3–30 additional heads of conidia; conidia hyaline and uniseptate with a broad distal and apiculate proximal end; chlamydospores, if present, yellow, round to oblong, single or in chains, intercalary or terminal.

Mycelium in nematode-infested culture usually prostrate, often fusing to form predaceous networks, constricting rings or adhesive aerial knots.

The 2 keys which follow can be used for the identification of the species of *Arthrobotrys* recognized as valid. The characteristics of 4 species, *A. anchonia* Drechs. (**1954**), *A. dolioformis* Soprunov (**1958**), *A. entomopaga* Drechs. (**1944b**) and *A. oviformis* Soprunov (**1958**) were taken from the literature.

Characteristics used in both keys are based on studies of isolates grown on maizemeal agar and incubated at 25 C. However, the first key is based on pure culture characteristics and the second on characteristics found in nematode-infested cultures.

The second key should be used only as a preliminary attempt at identification as characteristics vary much more widely in nematode-infested cultures than in pure cultures. Also, some characteristics such as branching of the conidiophores may not be evident in nematode-infested cultures.

Discussions of those species studied below follow the keys in alphabetical order.

KEY TO SPECIES OF ARTHROBOTRYS IN PURE CULTURE

1. Conidia produced in several whorls at swollen nodes along conidiophore.....2
1. Conidia produced at the apex of the conidiophore and its branches; occasionally weak nodal development.....8
2. Conidiophores branched.....3
2. Conidiophores unbranched.....5
3. Cells of conidia nearly equal in length; conidia not constricted at septum.....*A. arthrobotryoides*
3. Distal cell of conidia distinctly longer than proximal cell; conidia constricted at septum.....4
4. Conidia obovoid to pyriform; distal cell swollen, nearly globose..*A. oviformis*
4. Conidia elongate obovoid; distal cell not swollen.....*A. dolioformis*
5. Cells of conidia equal in length; conidia not constricted at septum.....6
5. Distal cell of conidia distinctly longer than proximal cell; conidia constricted at septum.....7
6. Conidiophore head irregularly swollen; conidia on wartlike sterigmata in a tight capitate head; conidia 15–27 μ long, 5–11 μ wide..*A. superba*
6. Conidiophore head regularly inflated; conidia on long sterigmata in loose capitate heads; conidia 15–28 μ long, 4–5 μ wide.....*A. entomopaga*
7. Conidia obovoid to pyriform; distal cell length 2 × proximal; conidia 15–30 μ long, 8–15 μ wide.....*A. oligospora*
7. Conidia elongate obovoid; distal cell length 1½ × proximal; conidia 18–45 μ long 8–15 μ wide.....*A. conoides*
8. Conidiophores unbranched.....9
8. Conidiophores branched.....11
9. Cells of conidia equal in length.....*A. dactyloides*
9. Distal cell of conidia distinctly longer than proximal cell.....10
10. Conidia obovoid, on short wartlike sterigmata; conidia 29–43 μ long, 15–19 μ wide.....*A. anchonia*
10. Conidia elongate ellipsoid, slightly curved, on long sterigmata; conidia 28–49 μ long, 8–16 μ wide.....*A. musiformis*
11. Conidiophore tip not swollen; conidia large (20–40 μ long), born on long sterigmata.....*A. robusta*
11. Conidiophore tip swollen; conidia small (11–22 μ long), born on wartlike sterigmata.....*A. cladodes*

KEY TO SPECIES OF ARTHROBOTRYS IN NEMATODE-INFESTED CULTURES

1. Predaceous organs consisting of sticky knobs.....*A. entomopaga*
1. Predaceous organs consisting of networks or constricting rings.....2
2. Constricting rings present.....3
2. Predaceous networks present.....4
3. Distal cell of conidia longer than proximal cell; conidia obovoid, 29–43 μ long, 15–19 μ wide.....*A. anchonia*
3. Cells of conidia equal in length; conidia elongate ellipsoid, 32–48 μ long, 7–9.5 μ wide.....*A. dactyloides*
4. Conidiophore tip swollen; head of conidia compact.....5
4. Conidiophore tip not swollen; head of conidia loose.....11
5. Conidia constricted at the septum.....6
5. Conidia not constricted at the septum.....9
6. Conidia obovoid to pyriform.....7
6. Conidia obconical to elongate obovoid.....8
7. Conidia 15–25 μ long, 7–12 μ wide, conidiophore usually nodular; groups of conidiophores forming in clumps.....*A. oligospora*
7. Conidia 22–33 (26.5) μ long; 10–15 (13) μ wide; conidiophore single, usually nodular or branched.....*A. oviformis*
8. Distal cell of conidia distinctly swollen; conidiophores may be nodular.....*A. conoides*
8. Distal cell of conidia not distinctly swollen; conidiophore may be nodular or branched.....*A. dolioformis*
9. Conidia elongate ovoid.....10
9. Conidia ovoid to obovoid, 12.6–32.2 (20.7) μ long and 4.2–12.6 (8.7) μ wide.....*A. arthrobotryoides*
10. Distal cell of conidia slightly tapered; conidia 10–18 μ long, 5–9 μ wide; conidiophore not nodular.....*A. cladodes*
10. Distal cell of conidia not tapered; conidia 16.8–26.5 μ long, 5.6–11.2 μ wide; conidiophore may have 2 nodes.....*A. superba*
11. Conidia slightly curved, formed in a loose head on long sterigmata; conidiophore simple.....*A. musiformis*
11. Conidia formed in a compact head on shorter sterigmata; conidiophores branched.....*A. robusta*

ARTHROBOTRYS ARTHROBOTRYOIDES (Berlese) Lindau, *in* Rabenhorst's Kryptogamen-Flora., p. 371. 1907.

Syn: *Cephalothecium roseum* Corda var. *arthrobotryoides* Berlese, Malpighia **1**: 245–246. 1888.

Didymozoophaga arthrobotryoides Soprunov & Galiulina, Mikrobiologiya **20**: 489–499. 1951.

Arthrobotrys superba Corda var. *irregularis* Mat., Recherches sur le développement de quelques Mucedinées. 1892.

Colony in pure culture white or pale rose, spreading rapidly; mycelium prostrate, hyaline, septate, highly branched, 2.5–5.5 μ wide, often forming circular rings from which conidiophores arise, sometimes form-

ing adhesive loops compounded into networks; aerial mycelium, appearing on plates as small "woollike" tufts often fusing longitudinally into coarse strands or rings above substratum before bearing conidiophores; conidiophores, arising in clumps from circular hyphae or singly from a single hyphae within 1 week, highly branched, 4–8 septate, 4.5–5 μ wide at base tapering to 1.5–3 μ wide just below swollen tip, reaching length of 200–400 μ at first node when originating from prostrate mycelium, 10–200 μ when originating from aerial mycelium, often elongating to form 2–8 nodes of conidia at irregular distances; conidiophore tip irregularly swollen, bearing up to 25 conidia in a single capitate head; conidia 12.6–32.2 (20.7) μ long, 4.2–12.8 (9.5) μ wide, solitary on blunt wartlike or branchlike sterigmata, 2-celled, ovoid to obovoid; distal cell slightly swollen; occasionally constricted at septum; distal end rounded; base apiculate; chlamydospores unknown.

Colonies in nematode-infested culture indistinct; mycelium prostrate, septate, hyaline, branched, 3–6 μ wide, forming adhesive loops often compounded into networks; conidiophores unbranched, 300–450 μ in length, 5–7 μ wide at base tapering gradually to 4–5 μ below apex, bearing single capitate head of 5–15 conidia, occasionally elongating to form 2 additional heads; conidia as in pure culture.

This organism was first described by Berlese in 1888 as *Cephalothecium roseum* Corda var. *arthrobotryoides* Berlese. This was probably due to a misinterpretation of conidiophore characteristics. After Matruchot redescribed conidial formation in *Cephalothecium* and *Arthrobotrys,* he transferred this variety to the genus *Arthrobotrys* as a synonym of *A. oligospora.* This was apparently done from the description since he gave no reference to any actual culture study. However, his writings indicate that he may in fact have handled material of *A. arthrobotryoides* as we know it today without realizing it. His account and illustrations of *A. superba* var. *irregularis* indicated that it was branched and nodular.

Lindau (1907) raised *A. arthrobotryoides* to specific rank but added nothing new to the previous description.

Drechsler (1937) studied *A. arthrobotryoides* and chose to follow Lindau's 1907 classification. He noted in his studies that this species did not always have localized nodes but that the conidia were often borne on sterigmata along an irregularly branched rachis.

Drechsler was also familiar with Matruchot's (1892) work. He concluded from Matruchot's description of *A. superba* var. *irregularis* that this isolate may have actually been *A. arthrobotryoides* because it had both irregularly spaced nodes and branched conidiophores.

This species appears to be most closely related in morphology to 2

species described by Soprunov (**1958**), *A. dolioformis* and *A. oviformis.* All three have branched nodular conidiophores, but their conidia differ in size and shape. A fourth species by Soprunov (**1958**), *A. kirghizica,* may be synonymous with *A. arthrobotryoides* but material was not available for study.

Material studied.—Unnumbered culture from Centraalbureau Voor Schimmelcultures, Baarn, Holland; Nos. 1 and 3 from soil and roots, Hackberry Glen, Riley Co., Kansas, Karen Haard, February 1963; no. 30 from mud, Spillway Park, Pollawatomie Co., Kansas, Karen Haard, August 1964; Nos. 40, 41, and 43 from soil near or in bog, Antique Bog, S.W. of Pellston, Emmet Co., Michigan, Karen Haard, July 1965; No. 44 from moss and rotten wood in maple forest, 1½ mi. E. Douglas Lake, Cheyboygan Co., Michigan, Karen Haard, July 1965.

ARTHROBOTRYS CLADODES Drechsler, Mycologia **29**: 4, 459–464. 1937.

Syn: *Trichothecium cladodes* Soprunov, Predaceous fungi—Hyphomycetes and their application in the control of pathogenic nematodes. 1958.

Colony in pure culture hyaline, spreading radially; mycelium prostrate, hyaline, septate, 2–6 μ wide, often fusing; conidiophores appearing 2–30 days after inoculation, erect, septate, very delicate, 150–350 μ in length, 3.5 μ wide at base tapering to 1.2–3 μ wide below irregularly swollen tip, highly branched, occasionally elongating to form 1–2 nodes of conidia after initial head; conidiophore tips irregularly swollen bearing 20–30 conidia on wartlike sterigmata in a tight capitate head; conidia 2-celled, 10–18 (15) μ long, 5–9 (7.5) μ wide, rounded at both proximal and distal ends with sharp apex at point of attachment; cells equal.

Mycelium in nematode-infested cultures prostrate, hyaline, septate, branched forming adhesive loops often compounded into networks; conidiophores non-nodular, unbranched, larger and more scattered than in pure culture; conidiophore tip irregularly swollen bearing 10–15 conidia on sterigmata; conidia as in pure culture; chlamydospores unknown.

Material studied.—No. 8415 from culture collection, U. S. Army Natick Laboratories.

ARTHROBOTRYS CLADODES VAR. MACROIDES Drechsler, Mycologia **36**: 2, 138–145. 1944.

Syn: *Trichothecium cladodes* var. *macroides* Sopr. Predaceous fungi—Hyphomycetes and their application in the control of pathogenic nematodes. 1958.

Colonies in pure culture hyaline to white, spreading radially; mycelium 1–6 μ wide, hyaline, septate and branched; conidiophores, appearing in 2–3 weeks, erect, hyaline, 3–7 septate, 75–300 μ in length, 3.5–7 μ wide at base tapering to a width of 2–3 μ just below swollen tip, highly branched and occasionally elongating to form 1–3 additional heads of conidia; conidiophore tip irregularly swollen bearing 5–20 conidia on wartlike sterigmata in a tight capitate head; conidia hyaline, uniseptate, elongate obovoid to oblong ovoid, 14–35 (20) μ long, 5.5–11.5 (7) μ wide; distal end broadly rounded; proximal end strongly pedicellate, 2 cells nearly equal in length.

Mycelium in nematode-infested culture prostrate, septate and hyaline, forming adhesive loops often compounded into networks; colony a profusion of erect, non-nodular unbranched conidiophores slightly larger than those in pure culture; conidiophore tip swollen bearing 5–15 conidia like those in pure culture.

Material studied.—Two unnumbered cultures from Centraalbureau voor Schimmelcultures (one identified as *A. conoides* and the other as *A. cladodes* var. *macroides*); No. 8416 from culture collection, U. S. Army Natick Laboratories.

Both varieties of *A. cladodes* differ from other species in having a combination of branched conidiophores, limited nodular development, and very small conidia. They differ from each other in conidia size and shape. *A. cladodes* var. *macroides* has larger, strongly pedicellate conidia while *A. cladodes* var. *cladodes* has conidia which average 5 μ shorter and which have a brief pointed apex. *A. cladodes* var. *macroides* is also reported to have resting bodies but this was not observed in the material used in this study.

ARTHROBOTRYS CONOIDES Drechsler, Mycologia **29**: 4, 473–477. 1937.

Colonies in pure culture white to yellow, spreading radially; mycelium hyaline, septate and branched producing conidiophores in 1–2 weeks; conidiophores unbranched, 4–8 μ wide at base tapering to a width of 2–3 μ at a height of 100–500 μ; conidiophore tip irregularly expanded to a width of 5.5–8.5 μ bearing up to 30 conidia in a tight capitate head before elongating to produce 3–12 additional heads; conidia elongate obovoid, 18–45 (26) μ long, 8–15.5 (11) μ wide, uniseptate, usually constricted at septum, broadly rounded at distal end and apiculate at proximal end; distal cell slightly swollen, 10–30 (15) μ long averaging $1\frac{1}{2}\times$ length of proximal cell; chlamydospores intercalary, round to oblong, single or in chains, abundant in old cultures; adhesive networks frequent in fresh pure culture.

Networks of single adhesive loops joined in a 3-dimensional pattern in nematode-infested cultures, more abundant than in pure cultures;

mycelium in colonies prostrate giving rise to scattered conidiophores; conidiophores 100–500 μ tall, non-nodular, with 7–15 conidia in single terminal capitate head; conidiophore tips swollen with sterigmata; average conidia 32 μ long, 13 μ wide with proximal cell 13 μ long; chlamydospores as in pure culture.

Arthrobotrys conoides appears most closely related to *A. superba* and *A. oligospora*. All 3 species have unbranched and nodular conidiophores. The main difference between these species is that *A. conoides* has obconical conidia, *A. oligospora* has pyriform conidia and *A. superba* has elongate ovoid conidia.

Material studied.—No. 7857, from Culture Collection, U. S. Army Natick Laboratories; No. 5, from soil, city dump near Manhattan, Riley Co., Kansas, Karen Haard, April 1963; No. 8, from soil, Wildcat Creek near Manhattan, Riley Co., Kansas, Karen Haard, April 1963; No. 22, from decayed leaves, Wildcat Creek near Manhattan, Riley Co., Kansas, Karen Haard, May 1963; No. 45, from rotten log covered with moss, 1½ miles E. Douglas Lake, Cheyboygan Co., Mich., Karen Haard, July 1965.

ARTHROBOTRYS DACTYLOIDES Drechsler, Mycologia **29**: 4, 482–487. 1937.

Syn: *Dactylaria dactyloides* Sopr., Predaceous fungi—Hyphomycetes and their application in the control of pathogenic nematodes. 1958.

Colonies in pure culture thin, hyaline, spreading radially; mycelium 2–6 μ wide, highly branched, septate and hyaline; conidiophores, appearing on both aerial and prostrate mycelium within 2½–3 weeks after inoculation, erect, non-nodular, unbranched, 3.5–5.5 μ wide at base tapering to 2.2–3.5 μ wide below tip, 200–400 μ tall with a terminal loose capitate head, occasionally elongating to produce 1 or 2 additional nodes or a single lateral side branch; conidiophore tip non-swollen bearing 4–10 sterigmata about 5 μ long and 1½–2½ μ wide each with a single conidium; conidia uniseptate, 2-celled, slightly curved, elongate ellipsoid, 32–45 (38) μ long, 6–10 (8) μ wide with proximal cell 15–25 (20) μ long; chlamydospores intercalary, round, single and yellow, up to 15 μ in diam; constricting rings with 3 arcuate cells on 2-celled stalk occasional in old desiccated cultures.

Colonies in nematode-infested cultures entirely of hyaline, septate, branched, prostrate mycelium; ring formation more prevalent than in pure culture, occurring in fresh cultures; rings borne directly on or in substratum at an angle perpendicular to surface with several often equally spaced on a single hyphae, usually all closing together with the

stimulation of one; conidiophores, conidia and chlamydospores as in pure culture.

A. dactyloides appears most closely related to *A. anchonia.* These 2 species are the only ones in this genus which form constricting rings. Also, they both have non-nodular, unbranched conidiophores. They differ from each other in the size and shape of conidia. *A. anchonia* has elongate obovoid conidia with unequal cells while *A. dactyloides* has elongate ellipsoid conidia with equal cells.

Material studied.—No. 2, from soil and roots, city dump, Manhattan, Riley Co., Kansas, Karen Haard, March 1963; No. 36, from wet greenhouse soil around *Marchantia,* Manhattan, Riley Co., Kansas, Karen Haard, October 1964; No. 46, in woods, Robinson and Pleasant View cross roads, Emmet Co., Michigan, Karen Haard, July 1965.

ARTHROBOTRYS MUSIFORMIS Drechsler, Mycologia **29**: 4, 477–482. 1937.

Syn: *Trichothecium musiformis* Sopr. Predaceous fungi—Hyphomycetes and their application in the control of pathogenic nematodes. 1958.

Candelabrella musiformis (Drechsler) Rifai & Cooke, Trans. Brit. Mycol. Soc. **49**: 1, 147–168. 1966.

Colony in pure culture white, spreading radially; mycelium hyaline, septate, branched and 3–5 μ wide; conidiophores, arising from both aerial and prostrate mycelium in 1–2 weeks, 200–400 μ in length, non-nodular, unbranched except in rare instances, 5.5–7 μ wide at base tapering to 2–3 μ wide below head; conidiophore tip not swollen, with 5–15 short branched sterigmata 9–21 μ long and 2–3 μ wide, each bearing a single uniseptate conidium thus forming a loose capitate head; conidia curved, elongate ellipsoid, 28–49 (35) μ long, 8–16 μ wide, broadly rounded at distal end and bluntly tapered at proximal end, with proximal cell 8–18 (11.5) μ long giving a distal to proximal cell ratio of 3:1, networks occasional in pure culture.

Colonies in nematode infested culture entirely of prostrate mycelium; mycelium hyaline, septate and branched bearing in profusion simple horseshoelike arches usually consisting of 4 cells; arches single or fused into simple 2-dimensional networks; conidiophores up to 200 μ in length bearing 5–15 conidia; conidia as in pure culture.

The distinguishing features of this species are the loosely capitate heads composed of 5–15 conidia produced on long, simple or branched sterigmata and the simple horseshoelike arches which compose the networks.

Rifai and Cooke (**1966**) transferred *A. musiformis* Drechsler to a new genus, *Candelabrella* Rifai & Cooke. This genus was erected on the basis of the candelabrum-like apical branching. Each branch is a long, thick conidial peg or sterigmata. However, *A. musiformis* is left in *Arthrobotrys* in this paper for the following reason. Of the 12 valid species of *Arthrobotrys,* two, *A. musiformis* and *A. entomopaga,* show this apical branching to the degree described in *Candalabrella.* One species, *A. robusta* Drechsler, has sterigmata too long to be classified as wartlike and too short for *Candalabrella* and another species, *A. arthrobotryoides,* shows both the wartlike sterigmata and the long thick conidial peg as well as rachis-type and regular branching. The other 8 species have different lengths of wartlike sterigmata. Due to the intergradation of types, it would be extremely difficult to find a dividing point between the 2 genera. Therefore, I would propose that *Candelabrella* be placed in synonomy with *Arthrobotrys.* The second species in this genus, *C. javanica* Rifai & Cooke has not been studied at this time but it seems probable that this will be included in *Arthrobotrys* in the future.

Material studied.—Unnumbered, from Centraalbureau voor Schimmelcultures, Baarn, Holland; No. 47, from duff in Warner Park, Manhattan, Riley Co., Kansas, Richard Haard, June 1965.

ARTHROBOTRYS OLIGOSPORA Fresenius, Beitrage zur Mykologie. 1850.

Syn: *Didymozoophaga oligospora* Sopr., Mikrobiologiya **20**: 489–499. 1951.

Arthrobotrys superba Corda var. *oligospora* Matr., Recherches sur le développement de quelques Mucedinées. 1892.

Arthrobotrys rosea Massee, J. Royal Microscop. Soc. **5**: 758–759. 1885.

Colonies in pure culture white to yellow, spreading radially; mycelium 1.5–3 μ wide, hyaline, septate and branched; conidiophores, arising singly or in groups from either aerial or prostrate mycelium in less than a week, unbranched except in rare instances, 5–7 μ wide at base tapering to 2–4 μ at height of 200–500 μ where first of 20–30 heads of conidia forms; conidiophore tip and nodular areas swollen to 4–6 μ bearing 5–20 conidia on wartlike sterigmata in a tight capitate head; conidia 16.5–29.5 (24.4) μ long, 8.4–15.5 (13.6) μ wide, pyriform, constricted at septum, with apiculiform base; distal cell swollen; proximal cell 4.2–11.2 (8.7) μ long; ratio of distal cell to proximal 2:1; adhesive networks occasional in fresh cultures.

Mycelium in nematode-infested cultures prostrate and hyaline, forming adhesive hyphal loops which fuse into networks; conidiophores,

forming in clusters of 3–12, with 1–4 nodes of conidia; conidia 15–25 μ long, 7–12 μ wide, slightly smaller than in pure culture with distal cell less swollen; septum constricted; proximal end apiculate; chlamydospores yellow, spherical or cylindrical, intercalary, single, or in chains, 11.5–18.5 μ in diam or approximately 8 × 20 μ if oval.

After Fresenius described this species in 1850, Massee described another in 1885 which he called *Arthrobotrys rosea*. Massee's description is as follows.

"*Arthrobotrys rosea* tufted; pale rose colour; fertile flocci erect, sparingly septate, with three to five swollen nodes at equal distances, each node bearing a globose head of conidia; conidia broadly obovate, uniseptate, slightly constricted at the septum, apical segment largest, base apiculate."

A. rosea was first considered a synonym of *A. oligospora* by Matruchot (**1892**). Drechsler (**1937**) also studied it and suggested that it should be put into synonomy. His reasons were that this species is nodular and has obovate conidia which are constricted at the septa. Also the illustration depicts the same proportions between the basal and distal cells as is given for *A. oligospora*. Because of this, it is listed here as a synonym.

Material studied.—Unnumbered from Centraalbureau voor Schimmelcultures, Baarn, Holland; No. 6, from mushroom bed, Kansas City, Mo., Richard Haard, 1964; Nos. 48, 49, and 50 from soil of barnyard, E of UMBS, Cheboygan Co., Mich., Karen Haard, July 1965; No. 51, from White House Landing near Emerson, Mich., Karen Haard, July 1965; No. 52, from rotten wood in Bryants Bog, Cheboygan Co., Mich., Karen Haard, July 1965.

ARTHROBOTRYS ROBUSTA Duddington, Trans. Brit. Mycol. Soc. **34**: 598–600. 1951.

Syn: *Trichothecium robustum* Sopr., Predaceous fungi—Hyphomycetes and their application in the control of pathogenic nematodes. 1958.

Colony in pure culture white, spreading radially; mycelium hyaline, septate, highly branched, 2–7 μ wide with a profusion of conidiophores; conidiophores, appearing in less than a week after inoculation, highly branched, 100–500 (200–300) μ in length, 4–6.5 μ wide at the base tapering to 2.4 μ below head; conidiophore tip and branch apexes nonswollen, bearing 5–15 conidia on long sterigmata or 1–3 conidia when occasionally elongating to form a second node of 5–15 conidia; conidia uniseptate, elongate ovoid to elongate obovoid with definite pedicle, 21–40 (30.7) μ long, 7–12.5 (9.7) μ wide with proximal cell 9.8–24

(17.5) μ long; ratio of distal to proximal cell 1:1 with distal cell slightly swollen; septum not constricted; chlamydospores not observed.

This isolate has not been grown in nematode-infested culture. It has died every time nematodes were introduced into a culture.

This isolate varies from Duddington's in the size and shape of the conidia, but other characteristics agree with those of the description.

Material studied.—No. 8416, from culture collection, U. S. Army Natick Laboratories.

ARTHROBOTRYS SUPERBA Corda, Pract-Flora Europaeischer Schimmelbildungen. 1839.

Syn: *Didymozoophaga superba* Sopr., Mikrobiologiya **20**: 489–499. 1951.

Arthrobotrys drechsleri Sopr., Predaceous fungi—Hyphomycetes and their application in the control of pathogenic nematodes. 1958.

Colony in pure culture white to pale rose, spreading radially; mycelium septate, hyaline, branched, 1.5–5.5 μ wide; conidiophores, appearing in 1–2 weeks from both aerial and prostrate mycelium, 50–200 μ long if from aerial mycelium or 200–500 μ long if from prostrate, 3.5–5 μ wide at base tapering to 1.5–4 μ below tip, unbranched, nodular, often elongating past first head to form 20–30 more capitate heads of conidia; conidiophore tips swollen to 4.5–8.5 μ wide bearing 5–15 conidia on short wartlike sterigmata in a whorled pattern, often becoming so heavy with conidia that conidiophore bends under weight; conidia uniseptate, hyaline, oblong ovoid, broadly rounded at distal end, tapered at proximal end, terminated in short apex, 13.5–26.5 μ long, 5.6–11.2 (8.2) μ wide with proximal cell 7–12.6 (10) μ long; ratio of distal cell length to proximal 1:1, septum less constricted and apex less pointed than Corda's illustration.

Mycelium in nematode-infested culture prostrate forming adhesive loops often compounded into networks; conidiophores erect, 100–300 μ long, 3.5 μ wide at base, 2–3.5 μ wide at tip, unbranched with single terminal head of conidia or, occasionally 2 but never 3 heads; conidia as in pure culture.

Material studied.—Nos. 1688 and 7365, from culture collection, U. S. Army Natick Laboratories; No. 23, from decaying wood, Wildcat Creek, Manhattan, Riley Co., Kansas, Karen Haard, April 1963; No. 53, from rotten wood, in woods, south bank of pond area at Tuttle Creek; Riley Co., Kansas, Karen Haard, June 1965.

EXCLUDED SPECIES

The species listed in this section are excluded from the previous section for one or more of the following reasons: 1) their descriptions lack details necessary for accurate identification of material, (Nos. 1, 3, 4, 5); 2) appear synonymous with established species, (No. 2); or 3) differ from other species to the extent that they probably belong in other genera, (No. 6). Material, including the type specimens of these species, was unavailable at this time.

1. *Arthrobotrys deflectans* Bresadola, Annales Mycologici **1**: 2, 128. 1903.
2. *Arthrobotrys kirghizica* Sopr., Predaceous fungi—Hyphomycetes and their application in the control of pathogenic nematodes. 1958. Syn: *Didymozoophaga kirghizica* Sopr., Mikrobiologiya **20**: 6, 489–499. 1951.
3. *Arthrobotrys longispora* Pr., Linnaea **26**: 708. 1853.
4. *Arthrobotrys recta* Pr., Linnaea **24**: 128. 1851.
5. *Arthrobotrys staminicola* Pidoplichko, Mikrobiologichnii Zhurnal **9**: 55. 1948.
6. *Arthrobotrys stilbacea* Meyer, Bull. Soc. Mycol. Fr. **74**: 246. 1958.
7. *Arthrobotrys strangulans* Maupas, nomen nudum. *In* L. G. Seurat, Histoire naturelle des nematodes de la berberie. Premiere partie. Morphologie, développement: Ethologie et affinites des nématodes. Travaux du Laboratoire de Zoologie Générale. Université d'-Alger. Publications de la Faculté des Sciences. 1920.

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