PERSOONIA Published by the Rijksherbarium, Leiden Volume 14, Part 2, pp. 133-148 (1990)

NOTES ON MUCORALES—I Observations on Absidia

M.A.A. SCHIPPER

Centraalbureau voor Schimmelcultures, Baarn*

An account is given of species of *Absidia* maintained in the CBS collection. Cultures were studied on the basis of morphology, temperature relations and mating results. Synonymy is concluded for *A. atrospora*, *A. griseola*, and *A. hyalospora* with *A. blakesleeana; A. hesseltinei* with *A. corymbifera*. Mating activity was strong in the subgenus *Mycocladus*, weak or absent in the subgenus *Absidia*, under the test condition. A key to the species is included.

All strains of *Absidia* Tiegh. in the CBS collection, maintained in a lyophilized condition since 1962 or later, were checked for viability and identity. The opportunity was taken to commence a general survey of the genus.

A monograph of the genus Absidia was published by Hesseltine & Ellis (1964, 1966) and Ellis & Hesseltine (1965, 1966). More recent studies on Absidia isolates are by Váňová (1980, 1983, 1985). She presented well documented and profusely illustrated papers on representatives of the genus in Czechoslovakia. Unfortunately I am not familiar with the Czech language used in descriptions and discussions; a key to the treated species, in English, was added.

All available cultures were compared with the original descriptions of the species and with the descriptions of Hesseltine & Ellis (l.c.). The subdivision of the genus, as proposed by Hesseltine & Ellis, in the subgenera *Mycocladus* (Beauverie) Hesselt. & J.J. Ellis and *Absidia* Tiegh. is followed. A secondary grouping of species in the subgenera is used to show further relationships. The taxonomic positions of (new) species not included in the above monograph were studied. Mating experiments to trace eventual synonymy of morphologically similar species were part of the study.

The value of colony colour is discussed, as it may cause confusion in identification of *Absidia* species. Special attention is also given to the occurrence of giant-cells in the mycelium of, in particular, *Absidia blakesleeanus* Lendn. and *A. corymbifera* (Cohn in Lichtheim) Sacc. & Trott.

CLOSELY RELATED TAXA

The genera Apophysomyces Misra and Gongronella Ribaldi were studied along with Absidia to decide their status in relation to Absidia. Apophysomyces is close to Absidia in general

* Address: P.O. Box 273, 3740 AG Baarn, The Netherlands.

morphology. Zygospores are unknown. The single species *Apophysomyces elegans* Misra & al., shows optimal sporulation at 33°C, the growth maximum is at 40°C. At 25°C growth is slow, sporulation poor and sporangia often sterile. For sporulation yeast powder-soluble starch agar (Emerson's medium) is better than malt agar. This species is treated here as distinct from *Absidia*.

Gongronella with the species G. butleri (Lendn.) Peyronel & Dal Vesco and G. lacrispora Hesselt. & J.J. Ellis is regarded as a separate genus.

Mucor faisalabadensis.— The general morphology of the species Mucor faisalabadensis Mirza & al. place it between Mucor Mich.: Fr. and Absidia. Its apophysate piriform sporangia are characteristic of species of Absidia. As in the subgenus Mycocladus Hesselt. & J.J. Ellis, M. faisalabadensis has unadorned suspensors, gradually enlarging sporangiophores which show a darker colouring just below the sporangia, as well as giant-cells in the substrate. The temperature-growth relation $(15-40 \text{ (and } 45^\circ \text{C}))$ differs from Mucor, in which only few species grow and sporulate well at 40°C and only slowly at 15°C, e.g. Mucor indicus Lendn., M. prayagensis Mehrotra & Nand ex Schipper and M. variabilis Sarbhoy.

It is not characteristic of *Absidia* having sporangiophores which arise from the substrate, stolons and rhizoids absent and distinctly stellate zygospores as seen, in species of *Mucor*.

METHODS

As a routine, cultures were grown on two media (beerwort agar, potato-dextrose agar) and at various temperatures (between 15°C and 45°C).

In addition strains were contrasted with intraspecific and/or related interspecific partners.

The media used are: (i) beerwort agar containing 4% sugar, (ii) potato-dextrose agar (PDA) containing 20 g dextrose (1 l), (iii) beerwort agar with 20 or 40% saccharose added, (iv) czapek agar containing 30 g saccharose (1 l). For the preparation of media see 'CBS course of mycology' (Gams & al., 1987).

COLONY COLOUR IN SPECIES OF ABSIDIA

Traditionally, Absidia glauca Hagem and A. coerulea Bainier are distinguished by the colour of their young colonies; bluish-green in the former, versus bluish-purple in the latter.

Unfortunately, in practice the choice is often problematic. The colour is more intense on PDA, rice and bread, than on beerwort agar, more distinct in slant cultures then in petri dish cultures. No influence of temperature (15°C, 25°C, 30°C) was observed. Aging cultures of both species are grey. Of the strains studied, only a few showed distinctive tinges in the young colonies, the majority were greyish and indistinctive.

Tentative tests to extract and identify the colouring-matter by thin-layer-chromatography were unsuccessful. It seems that the compound is cellwall-bound (aerial hyphae; personal communication Dr G. W. van Eijk).

The closely related, slightly smaller, A. californica J.J. Ellis & Hesselt. does not have a greenish or bluish tinge in young colonies, but is greyish initially. Aerial hyphae beset with

dark droplets as occur in A. glauca, A. coerulea, and A. macrospora Váňová were not observed in A. californica. Absidia macrospora has a greenish tinge when young.

Another group of related species in which greenish and bluish violet tinges occur is *Absi*dia cylindrospora Hagem, *A. spinosa* Lendner, and *A. anomala* Hesselt. & J.J. Ellis. The changeable nature of the colouring in these species is shown below.

Absidia cylindrospora (6 strains) on PDA at 15°C bluish-grey, on PDA at 30°C yellowish grey, on beerwort agar at 25°C brownish or greenish grey.

Absidia spinosa (4 strains) on PDA at 15°C, one strain brownish grey, one strain greenish grey, and two strains bluish grey; on beerwort agar (25°C) all were brownish-greenish grey.

Absidia anomala, the single strain available was violet under all conditions of this study. A third group producing bluish-greyish pigments consists of Absidia blakesleeana Lendn.,

A. atrospora Naganishi & Hirahara, A. hyalospora (Saito) Lendn., A. griseola Naganishi & Hirahara, A. hesseltinei Mehrotra, and A. corymbifera (Cohn in Lichtheim) Sacc. & Trott. Young colonies on beerwort agar (25°C) are bluish grey in A. blakesleeana and A. griseola, deep bluish grey in A. atrospora and A. hyalospora, pale grey in A. corymbifera and A. hesseltinei.

When these osmo-tolerant species were grown on high sugar concentrations, it was observed that colonies on beerwort agar with 20% and 40% additional saccharose $(25^{\circ}C)$ showed a slightly different colouring: bluish grey in part of the *A. blakesleeana* strains and in *A. hyalospora*, slightly darker in *A. griseola*, deep bluish grey in other strains of *A. blakesleeana*, while deep violet-grey in *A. atrospora*.

So, colony colour is a useful characteristic in species of *Absidia*, but variable with conditions and not consistently present.

THE GENUS ABSIDIA

Absidia was characterized according to van Tieghem (1876) by stolons with rhizoids; by sporangiophores bearing apophysate piriform sporangia arising, mostly in small groups, from the elevated parts of the stolons (not opposite rhizoids); and by zygospores enveloped in appendages from the suspensors.

Since the characterization of the genus *Absidia* by van Tieghem (l.c.), material has been described fitting the above asexual features, but lacking appendages on suspensors. See Hesseltine & Ellis (1964) for a historical review of name changes and divisions of the genus.

The asexual condition is in most species the usual appearance; transferring species with an unadorned sexual state to a different genus might be very confusing for identifications, even though distinguishing secondary characters exist (see below).

In this paper the subdivision of the genus after Hesseltine & Ellis (1964) is followed: subgenus *Mycocladus* (Beauverie) Hesselt. & J.J. Ellis for species with free zygospores, and subgenus *Absidia* for species with zygospores enveloped in appendages from the suspensors, as described by van Tieghem (l.c.).

Furthermore, species belonging to the subgenus *Absidia* have been grouped according to similarity in shape of sporangiospores, arrangement of sporangiophores, maximum temperature for growth, and temperature range for sporulation. These groups are indicated here with A, B, C, etc.

P E R S O O N I A --- Vol. 14, Part 2, 1990

KEY TO THE SPECIES OF ABSIDIA

1a.	Colonies 40 mm or less in diam., in a month at 25°C; sucker-like branches in the substrate mycelium
	(species of uncertain position)
	Colonies usually filling petridish (90 mm diam.) in a few days; sucker-like substrate hyphae absent . 3
2a.	Homothallic zygospores present at 25°CA. parricida (Fig. 6a-c)
	Zygospores absent (unknown)
3a.	Determinate growth of the fertile aerial hyphae, generally ending in a large piriform sporangium; good
	growth at 36°C 4
b.	Indeterminate growth of the fertile aerial hyphae; typically no growth at 36°C
	Stolons and rhizoids absent; sporangiophores arising from the substrate (excluded from Absidia)
b.	Stolons and rhizoids present; sporangiophores arranged in random fashion on the stolons; whorls or ver-
	ticils not obvious
5a.	Sporangiospores subglobose, partly with roughened walls; at 45°C growth insignificant to absent . 6
b.	Sporangiospores subglobose to ellipsoidal or ellipsoidal-cylindrical, smooth; at 45°C rather good growth
	A. corymbifera (Fig. 2)
ба.	Sporangiospores globose to broadly ellipsoidal, 5-10 µm diam.
	A. blakesleeana var. atrospora (Fig. 1q-t)
b.	Sporangiospores subglobose, mostly 5-6 µm diam A. blakesleeana (Fig. 1)
7a.	Sporangiospores globose or short ellipsoidal
b.	Sporangiospores cylindrical or lacrimoid-cuneate
8a.	Sporangiospores globose-short ellipsoidal or slightly angular; sporangiophores both of the usual Absi-
	dia-type and single, short sporangiophores in series along stolons
	(subgenus Absidia group F) A. repens (Fig. 5n-h)
b.	Sporangiospores globose; sporangiophores of one type only (subgenus Absidia group A) 9
	Columellae with projections of intricate shape A. macrospora (Fig. 3j, k)
	Columellae with a single apical projection 10
10 a .	Sporangia up to 35 µm diam A. californica (Fig. 3d-f)
b.	Sporangia up to 50 μm diam 11
11a.	Young colonies bluish A. coerulea (Fig. 3a-c)
b.	Young colonies greenish (see text) A. glauca (Fig. 3g-i)
12a.	Sporangiospores lacrimoid-cuneate (subgenus Absidia group E) A. cuneospora (Fig. 5f, g)
	Sporangiospores cylindrical with rounded ends
13a.	Sporangiospores variable in size $(3-6 \times 2-3.5 \mu\text{m})$
	(subgenus Absidia group C) A. heterospora (Fig. 5a-c)
b.	Sporangiospores up to $5 \times 2.5 \ \mu m$
	At 30°C no growth; optimal at 15°C (subgenus Absidia group D) A. psychrophila (Fig. 5d, e)
	At 30°C growth; optimal at 20°C-24°C (subgenus Absidia group B) 15
	Homothallic zygospores present 16
b.	Zygospores absent
	Suspensors unequal, mono-appendiculate
	Suspensors equal, bi-appendiculate A. spinosa var. biappendiculata
	Zygospores up to 70 µm diam A. spinosa (Fig. 4j-m)
	Zygospores up to 80(-120) µm diam A. anomala (Fig. 4n-p)
	Whorls of 5 or more sporangiophores quite common 19
	Whorls of more than 3 sporangiophores rare
	Sporangiophores unequal in length A. fusca (Fig. 4g-i)
	Sporangiophores equal in length
	Sporangiospores $4-5 \times 2-2.5 \ \mu m$
	Sporangiospores 4 \times 2 μm
	Colonies (malt extract agar, 25°C) rather pale brownish-greenish grey A. cylindrospora (Fig. 4a-c)
b.	Colonies (malt extract agar, 25°C) dark brownish-greenish grey A. cylindrospora var. nigra

ABSIDIA SUBGENUS MYCOCLADUS (BEAUVERIE) HESSELT. & J.J. ELLIS

Zygospores not with appendaged suspensors.

Other characters.—Growth determinate with aerial hyphae generally ending in a large piriform sporangium. Sporangiophores arranged in random fashion on the stolons; whorls or verticils not obvious. Tendency to grow at elevated temperatures and also to produce zygospores at higher temperatures (typically at 31°C). (After Hesseltine & Ellis, 1964).

Since zygospores are unknown in species of which only one strain is available, the additional characters, such as growth at 37 °C., were used to indicate the taxonomic position.

Absidia parricida Renner & Muskat ex Hesselt. & J.J. Ellis, a homothallic species with unadorned zygospores was not considered here, in view of its psychrophilic nature and other features at variance with the above.

ACCEPTED SPECIES

Absidia atrospora Naganishi & Hirahara, A. blakesleeana Lendn., A. griseola Naganishi & Hirahara, and A. hyalospora (Saito) Lendn., with subglobose sporangiospores, some with roughened walls; at 45°C growth insignificant to absent, at 36°C growth and sporulation.

Absidia corymbifera (Cohn in Lichtheim) Sacc. & Trott. (syn: A. ramosa (Lindt) Lendn.) and A. hesseltinei Mehrotra, with subglobose to ellipsoidal or ellipsoidal-cylindrical, smooth sporangiospores; and at 45°C rather good growth.

MATERIAL STUDIED (all cultures from the CBS)

Absidia blakesleeana: CBS 100.28, 100.36, and 102.36. — Tentatively designated as A. blakesleeana ('A. aff. blakesleeana'): CBS 647.78, 648.78, and 420.70.

Absidia atrospora: CBS 518.71.

Absidia griseola: CBS 519.71. Absidia hyalospora: CBS 173.67.

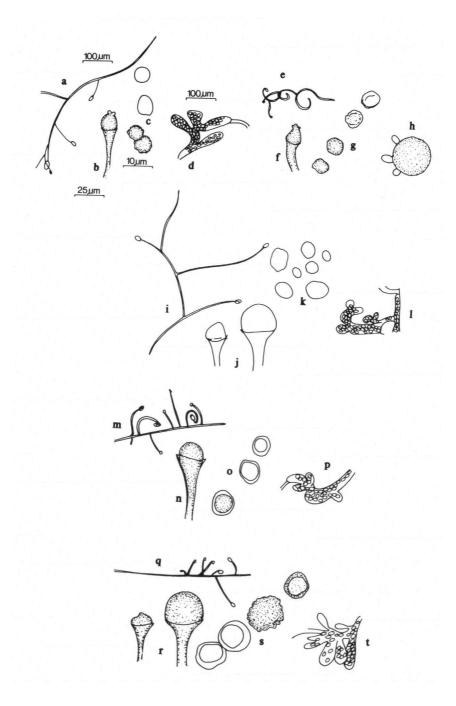
Austana nyaiospora. CB3 175.07.

Absidia corymbifera: CBS 100.17, 100.24, 100.31, 103.35, 102.48, 100.49, 100.51, 101.51, 100.55, 101.55, 269.65, 270.65, 271.65, 582.65, 291.66, 713.74, 429.75, 223.78, and 649.78. Absidia hesseltinei; CBS 958.68.

TEMPERATURE-GROWTH REACTIONS

Slant cultures (beerwort agar) were placed at 15° C, 36° C, and 45° C immediately after inoculation. Results were noted after three days for 36° C and 45° C, and after twelve days in the case of cultures at 15° C. The slants had been inoculated with a tiny piece of inoculum (substrate with airial mycelium and spores) and a streak of the needle upwards. It was found that both at 15° C and 45° C sporulation might occur at the very edge of the slant, though little or no growth could be observed near the inoculum. This indication of possible osmophily was checked by culturing the strains on beerwort agar with 20% and 40% saccharose respectively, at 25° C.

At 45°C there was rather good growth in all strains of A. corymbifera and A. hesseltinei, slightly restricted, low growth in A. griseola, no growth near the inoculation piece, but sporulation at the very edge of the slant, in A. blakesleeana, and no growth at all in A. aff. blakesleeana, A. atrospora, and A. hyalospora.



At 36°C all strains studied showed growth and sporulation. The strains of A. aff. blakesleeana grew rather slowly and sporulation was poor.

At 15°C growth was insignificant in A. atrospora and A. hesseltinei, also insignificant, but with slight sporulation at the agar edge in A. blakesleeana, A. hyalospora, and most strains of A. corymbifera; while growth was restricted in A. aff. blakesleeana and A. griseola, and also restricted but with sporulation in some strains of A. corymbifera.

INFLUENCE OF SUGAR CONCENTRATION OF THE MEDIUM (beerwort slants with 20% and 40% saccharose, at 25°C)

All strains of Absidia atrospora, A. blakesleeana, A. griseola, and A. hyalospora had in common that after three days the development of aerial mycelium was less on media with 40% than on media with 20% saccharose. Among these strains, three were noticeable due to the presence of abundant young sporangia, both on slants with 40% and 20% saccharose, namely A. atrospora, A. griseola, and A. aff. blakesleeana (CBS 647.78). After two weeks, all colonies were well developed and no difference was obvious between cultures of each strain on the two media.

The strains of A. corymbifera and A. hesseltinei had in common that after three days development was more profuse on beerwort agar with 20% than with 40% saccarose. But after 10 days the slants with 40% saccarose were either a darker grey (good sporulation!) than with 20% saccarose, or alike.

GIANT-CELLS

Irregularly swollen, droplet-filled, substrate hyphae, sometimes swollen up to the size of 'giant-cells' are quite common in a number of *Absidia* species, especially in *A. blakesleeana* and *A. corymbifera*. Shape and size of the swollen parts vary from modest to elaborate with projecting parts (Fig. 1).

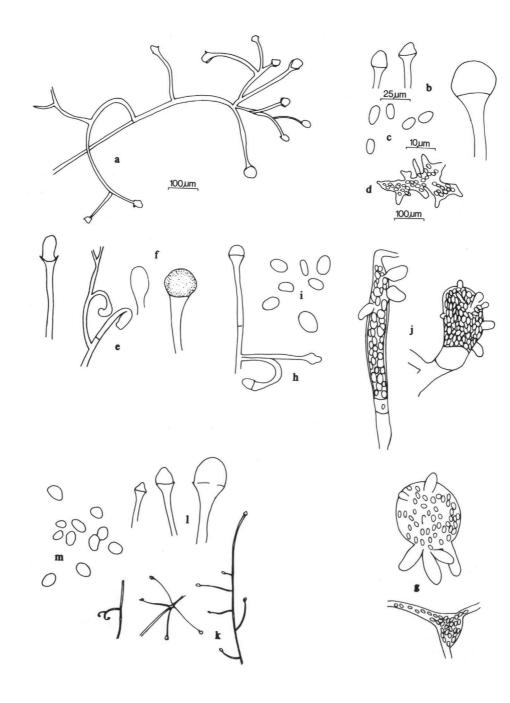
Generally, giant-cells only occur in substrate hyphae, but in strains CBS 420.70 and 648.78 (A. aff. *blakesleeana*), and CBS 223.78 (A. *corymbifera*) abundant, ornamented, giant-cells were also formed in the aerial mycelium.

MATINGS (on malt yeast agar at 33°C)

The three strains CBS 100.28 (+), 100.36 (-), and 102.36 (-) of A. blakesleeana, morphologically similar, are able to produce zygospores with the appropriate partner.

No mating reaction was observed in contrasts of the strains CBS 420.70, 647.78, and 648.78, of A. aff. blakesleeana, either with A. blakesleeana (+) or (-) or among each other.

Fig. 1. Absidia blakesleeana (sensu lato). — a-d. Strain CBS 100.36. — a. Sporangiophores on the stolon. — b. Columella. — c. Sporangiospores. — d. Giant-cell. — e-h. Strain CBS 420.70 (A. aff. blakesleeana). — e. Sporangiophores on the stolon. — f. Columella. — g. Sporangiospores. — h. Giant-cell. — i-l. Strain CBS 519.17 (A. griseola). — i. Sporangiophores on the stolon. — j. Columellae. — k. Sporangiospores. — l. Giant-cell. — m-p. Strain CBS 173.67 (A. hyalospora). — m. Sporangiophores on the stolon. — n. Columella. — o. Sporangiospores. — p. Giant-cell. — q-t. Strain CBS 518.71 (A. blakesleeana var. atrospora). — q. Sporangiophores on the stolon. — r. Columellae. — s. Sporangiospores. — t. Giant-cell.



Absidia griseola produced zygospores with CBS 100.36 (-). Absidia atrospora $\times A$. blakesleeana, CBS 100.36 (-) resulted in imperfect conjugations only. Contrasts of A. hyalospora $\times A$. blakesleeana (+) and (-) failed.

Absidia corymbifera (+) CBS 270.65, 100.49, 101.55, 223.78, 649.78, and the (-) strains CBS 271.65 and 100.55, were interfertile and so was A. hesseltinei × A. corymbifera, CBS 270.65 (+). Consequently, A. hesseltinei is a synonym of A. corymbifera.

Absidia griseola Naganishi & Hirahara (1970) was not validly published (nom. inval., I. C. B. N. art. 35). The strain CBS 519.71, A. griseola, received from H. Naganishi, differs from A. blakesleeana morphologically in the production of sporangia of a larger maximum size, which are powdery dry in appearance, with columellae which are mostly smooth and sporangiospores mostly subglobose but mixed with a few ellipsoidal ones, all light in colour; at 45°C slight growth occurs. Mated with CBS 100.36 (-), A. blakesleeana, zygospores were formed. Absidia griseola was published without a Latin diagnosis, and is based on an atypical specimen of A. blakesleeana, in some characteristics tending towards A. corymbifera.

Absidia atrospora Naganishi & Hirahara (1970) was published without Latin diagnosis (nom. inval., I.C.B.N. art. 35). The strain CBS 518.71, received from H. Naganishi, differs from A. blakesleeana mainly in the production of sporangiospores of a larger size and, mixed with the subglobose majority, some ellipsoidal ones. Mating tests of CBS 518.71 and A. blakesleeana, CBS 100.36 (-) revealed incomplete conjugations only. Though not interfertile, this strain is treated as a variety of A. blakesleeana that is newly described here.

Absidia blakesleeana Lendn. var. atrospora Schipper, var. nov. distinct from the var. blakesleeana in the production of globose to broadly ellipsoidal sporangiospores, 5-10 (-13) µm diam.

Absidia blakesleeana Lendn. var. atrospora Schipper, var. nov. A varietate blakesleeana differt sporangiosporis globosis vel late ovoideis, 5-10(-13) µm diam. Typus: CBS 518.71.

Absidia hyalospora (Saito) Lendn. was provided with a neotype and newly redescribed by Hesseltine & Ellis (1966). The strain derived from the neotype indicated by Hesseltine & Ellis is maintained at the CBS sub 173.67, A. hyalospora. The strain differs from A. blakesleeana in producing slightly larger sporangiospores. In A. blakesleeana strains grown on beerwort agar at 25 °C sporangiospores are $4-(5-)6 \mu m$ diam. (rarely larger; in strain CBS 173.67); sporangiospores are up to 7 μm diam., occasionally up to 10 μm , under the same conditions. Hesseltine & Ellis reported interfertility between A. hyalospora and A. blakesleeana. (Matings at the CBS failed to yield zygospores). The slight difference between the neotype of A. hyalospora and A. blakesleeana is not sufficient to justify maintaining these species separately.

Fig. 2. Absidia corymbifera (sensu lato). — a-d. Strain CBS 100.17. — a. Branching pattern sporangiophores on the stolon. — b. Columellae. — c. Sporangiospores. — d. Giant-cell. — e-g. Strain CBS 103.35. — e. Branching pattern sporangiophore. — f. Columellae. — g. Giant-cells. — h-i. CBS 100.55. h. Sporangiophores on the stolon with top-sporangium. — i. Sporangiospores. — j. Strain CBS 270.65., giant-cells. — k-m. Strain CBS 950.68 (A. hesseltinei). — k. Sporangiophores on the stolons, branching pattern. — 1. Columellae. — m. Sporangiospores.

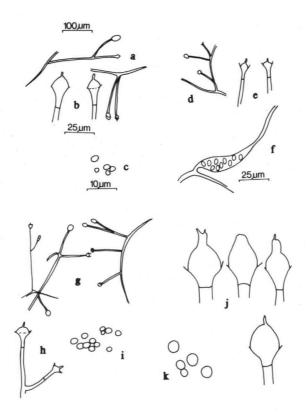


Fig. 3. Absidia subgenus Absidia, group A. — a-c. A. coerulea (CBS 104.08). — a. Sporangiophores on the stolons. — b. Columellae. — c. Sporangiospores. — d-f. A. californica (CBS 126.68). — d. Sporangiophores on the stolons. — e. Columellae. — f. Giant-cell. — g-i. A. glauca (CBS 101.08). — g. Sporangiophores on the stolons. — h. Columellae. — i. Sporangiospores. — j, k. A. macrospora (CBS 696.68). — j. Columellae. — k. Sporangiospores.

Absidia aff. blakesleeana.— Differences between the three strains (CBS 420.70, 647.78, and 648.78) tentatively identified with A. blakesleeana and the 'type' strain of the species (CBS 100.28), are in the more heavily branching sporangiophores with more circination, the brownish grey, powdery dry sporangia, the rather light colour of the sporangiospores, and the temperature reactions (no sporulation at the slant-edges at 45° C, slower growth and less sporulation at 36° C, and restricted growth at 15° C). Strain CBS 648.78 showed stronger sporulation under all conditions also at 15° C and on beerwort with 40% and with 20% saccharose. The strains CBS 420.70 and 648.78 produced abundant giant-cells with proliferations on aerial hyphae.

The deviations from the type characteristics are accepted as variability within the species. The unusual, very conspicuous aerial giant-cells, were also noted in a strain of A. corymbifera. Absidia corymbifera (19 strains) and A. hesseltinei (one strain) are very similar, thus A. hesseltinei is regarded as synonymous with A. corymbifera.

ABSIDIA SUBGENUS ABSIDIA

Zygospores surrounded with appendaged suspensors.

Other characters.— Growth of the aerial hyphae indeterminate. Most of the sporangiophores usually occur in whorls or verticils from stolons. Typically no growth at 37°C; zygospores formed at room temperature. (After Hesseltine & Ellis, 1964).

In this subgenus six groups of related species may be recognized.

GROUP A

Sporangiospores globose. Sporangiophores often in pairs, extensive whorls unusual. No growth at 36° C, growth and sporulation at 15° C- 30° C.

MATERIAL STUDIED (all cultures from the CBS)

Absidia californica J.J. Ellis & Hesselt.: CBS 126.68 and 314.78.

Absidia coerulea Bain.: CBS 104.08, 105.08, 101.28, 102.28, 103.28, 104.28, 100.32, 111.36, 100.38, 628.70A, and 628.70B.

Absidia glauca Hagem: CBS 100.06, 101.08, 102.08, 103.08, 100.48, 101.48, 100.59, 209.62, 422.70, and 423.70.

Absidia macrospora Váňová: CBS 696.68 and 697.68.

The colour of young colonies has been discussed before.

Matings on PDA at 25°C showed that all interspecific contrasts of A. glauca, A. coerulea, A. californica, and A. macrospora failed. The differences between A. coerulea, A. glauca, and A. californica seem mainly of a physiological nature. Zygospores of A. macrospora were not found.

Strain CBS 103.08, most probably a Lendner-strain, was originally designated as A. septata Tiegh. This species is homothallic, as can be judged from the original drawing. Lendner (1908) described A. septata 'after Fischer' with zygospores and azygospores. Zycha (1935) noted similarity with A. glauca, Ellis & Hesseltine (1965) with A. coerulea but for its homothallic nature. Strain CBS 103.08 did not show any sexual reactions and is morphologically identical with A. glauca. Whether the strain ever produced homothallic zygospores could not be traced.

GROUP B

Sporangiospores regularly cylindrical with slightly rounded ends. Sporangiophores in whorls. No (or neglectable) growth at 36° C; growth and sporulation at $15-30^{\circ}$ C.

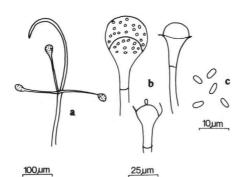
MATERIAL STUDIED (all cultures from the CBS)

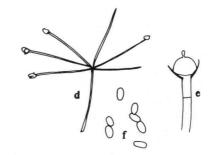
Absidia cylindrospora Hagem: CBS 100.08, 100.35, 101.35, 100.37, 101.37, 324.71, and 410.85.

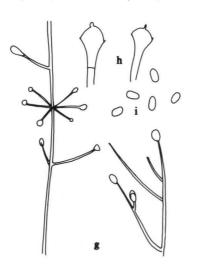
Absidia cylindrospora var. nigra Hesselt. & J.J. Ellis: CBS 127.68 and 315.78.

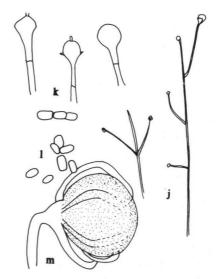
Absidia cylindrospora var. rhizomorpha Hesselt. & J.J. Ellis: CBS 153.63 and 154.63.

Absidia pseudocylindrospora Hesselt. & J.J. Ellis: CBS 100.62 and 480.66.

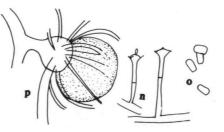








25,um



Absidia fusca Linnem.: CBS 102.35. Absidia spinosa Lendn.: CBS 106.08, 332.74, 222.78, and 316.78. Absidia spinosa var. biappendiculata Rall & Solheim: CBS 187.64. Absidia anomala Hesselt. & J.J. Ellis: CBS 125.68.

Colony colours have been discussed before.

Morphologically, Absidia cylindrospora var. nigra differs from the variety cylindrospora in the forming of darker colonies. In Absidia cylindrospora var. rhizomorpha whorls were mostly composed of three or two sporangiophores, but at the tips of stolons whorls of up to five sporangiophores occurred in strains of this variety. Furthermore the strains of this variety produced slightly larger sporangia, smooth columellae and also the maximum size of the sporangiospores was slightly larger than in the varieties cylindrospora and nigra. Though parts of the substrate hyphae were rather wide, 'rhizomorph-like' growth, as described by Hesseltine & Ellis (1964) was not observed. Some growth occurred at 36°C. On PDA 25°C, after seven days a 'rosette' colony was produced. Like the diagnostic good growth on Czapek agar, this indicates a physiological difference between the variety rhizomorpha and the varieties cylindrospora and nigra.

Absidia fusca was named after its dark colour, which, however, is produced only in older colonies, at lower temperatures, in the strain derived from the holotype which is the only one available. The species is related to A. cylindrospora, but different in the whorls of up to six sporangiophores (in seven day old colonies on beerwort agar, at 25°C), the mostly short (but rarely tall), not uncommonly branching sporangiophores, and the presence of swollen substrate hyphae filled with droplets. Compared with strains of A. cylindrospora development of A. fusca was rather slow at the studied temperatures (15°C, 25°C, and 30°C).

After the diagnosis Absidia pseudocylindrospora should be able to grow restrictedly, but sporulate well at 37 °C. However, no growth was observed at 36 °C on PDA. Morphologically, A. pseudocylindrospora differs from A. cylindrospora in the production of much darker colonies, and usually, more extensive whorls of sporangiophores (five being a quite common number).

Stain CBS 324.71, tentatively identified as A. cylindrospora, might be intermediate between A. cylindrospora and A. pseudocylindrospora: the sporangiophores are in extensive whorls, and insignificant growth occurs on PDA at 36°C, but poor on Czapek agar.

The homothallic counterparts of A. cylindrospora are A. spinosa and A. anomala.

Absidia anomala is very close to A. spinosa. Sporulation was scarce in A. anomala and zygospore production abundant, which interferes with a clear comparison of the species. In aging colonies of A. spinosa sporangiospores might be less uniform and reach a larger size, up to $5 \times 2.5-3 \mu m$ (cf. A. cylindrospora var. rhizomorpha).

Fig. 4. Absidia subgenus Absidia, group B. — a-c. A. cylindrospora (CBS 101.37). — a. Sporangiophores on the stolon. — b. Sporangium and columellae. — c. Sporangiospores. — d-f. A. pseudocylindrospora (CBS 480.66). — d. Sporangiophores on the stolon. — e. Columella. — f. Sporangiospores. — g-i. A. fusca (CBS 102.35). — g. Sporangiophores on the stolons. — h. Columellae. — i. Sporangiospores. j-m. A. spinosa (CBS 106.08). — j. Sporangiophores on the stolons. — k. Columellae. — l. Sporangiospores. — m. Zygospore. — n-p. A. anomala (CBS 125.68). — n. Columellae. — o. Sporangiospores. p. Zygospore.

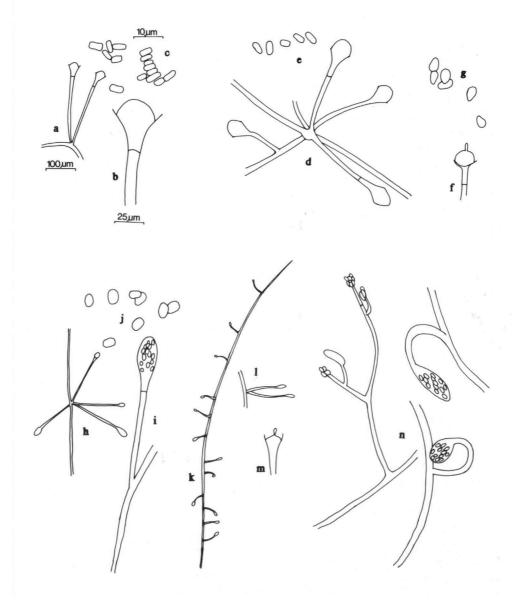


Fig. 5. Absidia subgenus Absidia, group C, D, E, F. — a-c. Group C, A. heterospora (CBS 588.74). — a. Sporangiophores on the stolon. — b. Columella. — c. Sporangiospores. — d, e. Group D, A. psychrophyla (CBS 128.68). — d. Sporangiophores, columellae. — e. Sporangiospores. — f, g. Group E, A. cuneospora (CBS 101.59). f. Columella. — g. Sporangiospores. — h-n. Group F, A. repens — h-j. Strain CBS 100.16 — h, i. Sporangiophores on stolons — j. Sporangiophores. — k-m. Strain CBS 101.32 — k, 1. Sporangiophores on stolons. — m. Columella. — n. Strain CBS 102.32, Sporangiophores on stolons.

Matings on PDA at 25°C demonstrated that strains of Absidia cylindrospora were intrafertile with one exception: CBS 324.71 (see above). This strain mated neither with A. cylindrospora (+) and (-) nor with A. pseudocylindrospora (+) and (-). In A. cylindrospora var. nigra, and A. pseudocylindrospora intrafertile partners were available.

The strains of A. cylindrospora var. rhizomorpha failed to yield zygospores, though they were received as mating partners (Hesseltine & Ellis, 1961). At the time of this study, no sexual reactions were observed.

Zygotes and mating reactions.— In Absidia fusca zygospores are unknown. Interspecific and intervarietal contrasts of A. cylindrospora, A. cylindrospora var. nigra. A. cylindrospora var. rhizomorpha, A. pseudocylindrospora, and A. fusca failed to show reactions. Homothallic zygospores are formed in Absidia spinosa, A. spinosa var. biappendiculata, and A. anomala.

Absidia spinosa and A. spinosa var. biappendiculata.— The zygospores of A. spinosa are borne between unequal suspensors, the larger one forming appendages; A. spinosa var. biappendiculata is distinct by producing equal suspensors, both forming appendages.

In A. anomala zygospores tended to be larger, and infrequently much larger than in A. spinosa.

GROUP C

A single species, *Absidia heterospora* Ling-Young, with irregular cylindrical sporangiospores, of varying sizes. The strains, CBS 101.29 and 588.74, showed a slight submersed growth at 30°C; growth and sporulation occurred at 15°C and 25°C; at 25°C globose and cylindrical-ellipsoidal sporangiospores were produced.

The species differs morphologically from A. cylindrospora in the production of columellae without distinct projections and in irregularly shaped sporangiospores. Zygospores are unknown. Interspecific contrasts were without result.

GROUP D

The single representative of this group, Absidia psychrophila Hesselt. & J.J. Ellis (one strain, CBS 128.68), is close to Absidia cylindrospora (group B) sporangiospores cylindrical with rounded ends; sporangiophores in whorls; different in temperature-growth range: at 30° C no growth, at 20° C and 25° C growth in 'rosette' colony, with sporangia but sporangiospores rather unequal at 25° C, cylindrical at 20° C, growth and sporulation at 15° C rather slow. Zygospores unknown; no mating reaction with A. cylindrospora (+) and (-) (which may be, at least partly, due to incompatibility of optimal temperature for mating).

GROUP E

A single species with lacrimoid-cuneate sporangiospores, Absidia cuneospora Orr & Plunkett, related to A. cylindrospora and A. spinosa, differing in the cuneate shape of the sporan-

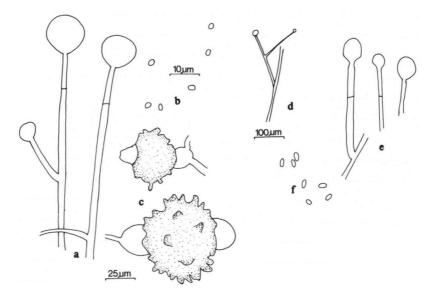


Fig. 6. Species of Absidia of uncertain position. — a-c. A. parricida (CBS 174.67). — a. Sporangiophores and columellae. — b. Sporangiospores. — c. Zygospores and suspensors. — d-f. A. zychae (CBS 104.35). — d. Sporangiophores. — e. Columellae. — f. Sporangiospores.

giospores. At 36°C the two strains (CBS 101.59 and 102.59) showed some growth but no sporulation; at $15^{\circ}C-30^{\circ}C$ growth and sporulation occurred.

The strains received as mating partners, did not react sexually on either PDA or hay infusion agar at 25°C, but produced a distinct yellow colony on the PDA medium, which is indicative of a sexual response. According to the first description of A. cuneospora, zygospores are up to 72 μ m diam., finely tuberculate or reticulate, and surrounded by branched, circinate appendages from the larger suspensor. In this respect it differs from A. cylindrospora and A. spinosa. Contrasts with A. cylindrospora (+) and (-) were unsuccessful.

GROUP F

The single species of this group, Absidia repens Tiegh., produces globose to short-ellipsoidal or slightly angular sporangiospores; smooth or slightly roughened; in the small sporangia dark coloured. Available strains: CBS 100.16, 101.32, and 102.32. This species differs from all other species of the genus in the production of two types of sporangiophores: the usual Absidia type and series of single, short, sporangiophores, straight or recurved, bearing small and narrow sporangia. At 30°C growth was restricted, though sporulation occurred; $15^{\circ}C-25^{\circ}C$ growth and sporulation occurred. The strains mentioned were intrafertile on PDA at 25°C; suspensors were either unequal, with only the larger appendaged or equal, with both appendaged.

SPECIES OF UNCERTAIN POSITION

Absidia parricida Renner & Muskat ex Hesselt. & J.J. Ellis (CBS 174.67) and Absidia zychae Hesselt. & J.J. Ellis (CBS 104.35) are both slow growing species with a very restricted temperature-growth range.

Absidia parricida is a mycoparasite. In pure culture development is slow, abundant suckerlike branches occur in the substrate-mycelium. Absidia zychae has the characteristics of a parasite (e.g. sucker-like branches) like A. parricida, but no potential host is known. Trials in this field failed: in mixed cultures with potential hosts, no parasitizing was observed. In A. parricida sporangiophores are borne on distinct stolons. In A. zychae sporangiophores arise either from distinct aerial hyphae (stolons) or from hyphae very near the substrate (surfacial substrate hyphae ?).

Z y g o s p o r i c s t a g e.— Absidia parricida shows homothallic zygospores, up to $65(-80) \mu m$ diam. with blunt projections, borne between equal, unadorned suspensors. In A. zycha zygospores are unknown, and interspecific contrasts were unsuccesful.

Temperature-growth response.— In A. parricida very restricted colonies occurred at 30°C; growth and sporulation were very slow at 20°C and 25°C; and no development was found at 15°C. In A. zycha no growth was found at 30°C, only very slow growth and sporulation at 25°C, while growth was extremely slow with restricted colonies and sporulation at 15°C.

ACKNOWLEDGEMENTS

The author is indebted to Dr G. Benny and Dr A. Onions for helpful comments. She wishes to thank Mrs L. van Dijk for skilful technical assistance; Mrs T. van den Berg and Mrs F. Snippe for their part in the preparation of the manuscript.

REFERENCES

ELLIS, J.J. & HESSELTINE, C.W. (1965). The genus Absidia: globose spored species. In Mycologia 57: 222-235.

— & — (1966). Species of Absidia with ovoid sporangiospores II. In Sabouraudia 5: 59-77.

GAMS, W., AA, H.H. VAN DER, PLAATS-NITERINK, A.J. VAN DER, SAMSON, R.A. & STALPERS, J.A (1987). CBS course of mycology. CBS, Baarn, Delft.

HESSELTINE, C. W. & ELLIS, J.J. (1961). Notes on Mucorales, especially Absidia. In Mycologia 53: 406-426.

— & — (1964). The genus Absidia: Gongronella and cylindrical-spored species of Absidia. In Mycologia 56: 568-601.

---- & ---- (1966). Species of Absidia with ovoid sporangiospores I. In Mycologia 58: 761-785.

LENDNER, A. (1908). Les Mucorinées de la Suisse. In Matér. Fl. Cryptog. Suisse 3.

NAGANISHI, H. & HIRAHARA, S. (1970). Two new species of the Absidia genus isolated from 'Kurone' developed during the manufacture of soy sauce Kojé. In Bull. Hiroshima Jogakuin agric. Coll. 20: 13-17.

TEGHEM, PH. VAN (1876). Troisième mémoire sur les Mucorinées. In Annls Sci. nat. (Bot.) Sér. VI, 4: 312-398.

VÁŇOVÁ, M. (1980). Genus Absidia van Tiegh. (Mucorales) in Czechoslovakia I. In Ceská Mykol. 34: 113– 122.

— (1983). Genus Absidia van Tiegh. (Mucorales) in Czechoslovakia II. In Ceská Mykol. 37: 151-171.

— (1985). Genus Absidia van Tiegh. (Mucorales) in Czechoslovakia III. In Ceská Mykol. 39: 85–96.

ZYCHA, H. (1935). Pilze II. Mucorinea. In Kryptog-Fl. Mark Brandenburg 6a.