

## THE GENUS ASCODESMIS (PEZIZALES, ASCOMYCETES)

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In this taxonomic revision of the genus *Ascodesmis* the monotypic family Ascodesmidaceae and the genus *Ascodesmis* are delimited and defined. Six species are recognized, described, and illustrated from living material and specimens preserved in herbaria. The typifications of the genus *Ascodesmis* and of the species *A. nigricans*, and *A. sphaerospora* are discussed without far-reaching consequences. *Ascodesmis nana* is described as new and the new name *Ascobolus perforatus* is proposed for *Ascodesmis canina* Jeng & Cain. A list of doubtful and excluded names is appended.

The genus *Ascodesmis* was established by van Tieghem in 1876 for *Ascodesmis nigricans* and *A. aurea*, two dung inhabiting fungi he considered to represent the elementary type of the Discomycetes. The generic name *Ascodesmis* was given by van Tieghem because the fruit bodies consist of an unprotected bundle of asci only. The growth and development of one of the species (*A. nigricans*) was studied in culture and described in detail.

Before *Ascodesmis* was established, species later regarded as members of this genus were classified under *Ascobolus* Pers. per Hook.

The Crouan borthers (1857) were the first to describe a species of *Ascodesmis*, naming it *Ascobolus microscopicus*. Their concept of the genus *Ascobolus* included all species of Ascomycetes with asci opening at their apex by an operculum.

Cooke (1877) included *Ascobolus microscopicus* in his new genus *Boudiera*.

Massee & Salmon (1902) described *Ascodesmis volutelloides* as a new species from England.

Hennings (1903) described the fungus of Claussen's (1905) developmental studies as *Boudiera claussenii*. Both Cavara (1905) and Dangeard (1907) recognized this as a species of *Ascodesmis*.

Bainier (1908) added two new species, *A. reticulata* and *A. echinulata*, from cultures in France.

Seaver (1916) recognized two species from North America, a species he identified as *A. microscopica* and a new species, which he named *A. porcina*. He (Seaver, 1928) also placed *Sphaeridiobolus* Boud. in the synonymy of *Ascodesmis*.

Le Gal (1949) contributed much to the knowledge of the genus *Ascodesmis* by giving good descriptions and illustrations of two species. By presenting an acceptable interpretation of *A. nigricans* and a description after the type of *A. microscopica*, she ended the numerous misapplications of these names and gave a solid base for later studies of the genus.

Obrist (1961) presented a study of *Ascodesmis* in which he published full descriptions of

four species, based on American material. *Ascodesmis macrospora* was newly described and *A. sphaerospora* was proposed as a new name for Seaver's misapplication of *A. microscopica*.

Jeng & Cain (1976) contributed, with *A. canina*, a new species from Venezuela.

In recent times, developmental studies of the fruit body by O'Donnell & al. (1976) and Delattre-Durand & Janex-Favre (1979) and electron microscopical studies of the spore ornamentation by Merkus (1973, 1976), also of the ascus wall by Samuelson (1978) and van Brummelen (1978, 1981) have strongly augmented our knowledge of *Ascodesmis*.

The small size of the fruit bodies, rarely surpassing two tenths of a millimeter, make the species of *Ascodesmis* difficult objects to find in natural habitats and thus unlikely to be collected frequently in nature. When brought into the laboratory, in cultures on dung or on artificial media, fruit bodies of *Ascodesmis* can be found more easily, especially when they aggregate and form crusts covering large parts of the substrate. So most records of species of *Ascodesmis* are from investigators who cultured them. In addition these fungi are ideal objects for studies on development, cytology, and ultrastructure because of their easy growth on artificial media and the absence of the protective parts of the receptacle, like excipulum and flesh.

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Grateful acknowledgement is made to Dr. J. A. von Arx, Centraalbureau voor Schimmelcultures, Baarn, and Madame Dr. J. Nicot, Mycothèque, Laboratoire de Cryptogamie, Muséum d'Histoire Naturelle, Paris, for cultures of *Ascodesmis*. Dried or living material has also been gratefully received from Dr. G. Arnold, Mrs. P. N. Bartlett, Dr. W. Gams, Dr. J. C. Krug, and Dr. M. J. Richardson.

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#### MATERIALS AND METHODS

**METHODS.**—Observations were made, whenever possible, on living material, but the major part of the material studied consisted of dried specimens.

The procedures and methods for cultivation, isolation, and microscopic examination were, in essence, the same as described earlier (van Brummelen, 1967).

For a more accurate indication of herbarium specimens, especially where the labelling is not wholly adequate, the customary abbreviations are followed by the author's revision numbers.

**HERBARIUM MATERIAL.**—Collections of dried specimens were received on loan from the following herbaria. The abbreviations are borrowed from Lanjouw & Stafleu (1964).

BPI,	National Fungus Collections, Beltsville, Maryland, U.S.A.
C,	Institut for Sporeplanter, Botansk Laboratorium, Copenhagen, Denmark.
DOAM,	Mycological Herbarium, Division of Plant Pathology, Ottawa, Canada.
E,	Royal Botanic Gardens, Edinburgh, Scotland, Great Britain.
FH,	Farlow Library and Herbarium of Cryptogamic Botany, Harvard University, Cambridge, Massachusetts, U.S.A.
H,	Botanical Museum, Helsinki, Finland.
HBG,	Staatsinstitut für allgemeine Botanik, Hamburg, Federal Republic of Germany.
K,	Herbarium, Royal Botanic Gardens, Kew, Great Britain.
L,	Rijksherbarium, Leiden, Netherlands.
M,	Botanische Staatssammlung, München, Federal Republic of Germany.
MPU,	Institut de Botanique, Université de Montpellier, Montpellier, France.
NY,	Herbarium of the New York Botanical Garden, New York, U.S.A.
PAD,	Instituto e Orto Botanico dell'Università, Padova, Italy.
PC,	Muséum d'Histoire Naturelle, Laboratoire de Cryptogamie, Paris, France
S,	Naturhistoriska Riksmuseet, Botaniska Avdelningen, Stockholm, Sweden.
TRTC,	Cryptogamic Herbarium, University of Toronto, Toronto, Canada.
U,	Institute for Systematic Botany, Utrecht, Netherlands.
URM,	Instituto de Micologia, Universidade do Recife, Recife, Pernambuco, Brazil.
W,	Naturhistorisches Museum, Wien, Austria.
ZT,	Institut für spezielle Botanik der Eidgenössischen Technischen Hochschule, Zürich, Switzerland.

#### DEVELOPMENT AND CYTOLOGY

Since their first discovery, species of *Ascodesmis* have been very attractive organisms for investigations on ontogeny, morphology, and cytology. Usually their ascospores germinate readily after inoculation on a wide scale of agar-media without special treatment. The whole life cycle may be finished within four days. No covering tissues of the receptacle, like excipulum or flesh will hide the initial stages from the eyes of the investigators.

In many cases the names given by investigators were wrongly applied. Therefore, the published developmental research on *Ascodesmis* listed below is, as far as possible, arranged according to the species concerned.

<i>Ascodesmis nigricans</i>	van Tieghem (1876) O'Donnell & al. (1976)
<i>Ascodesmis microscopica</i>	Zukal (1886; as <i>A. nigricans</i> ) Claussen (1905; as <i>Boudiera clausenii</i> ) Dangeard (1903a, b; 1907; as <i>A. nigricans</i> )
<i>Ascodesmis sphaerospora</i>	Swingle (1934; as <i>A. nigricans</i> ) O'Donnell & al. (1976) Delattre-Durand & Janex-Favre (1979; as <i>A. microscopica</i> )

All species studied thus far are homothallic.

Dangeard (1903b) observed four chromosomes in the mitoses of *A. microscopica*.

The development of the different species does not show essential differences. After germination of the ascospores, a septate mycelium with multinucleate cells is formed in which the growth is circular radiating. No conidia or spermatia have been found on the mycelia. Under favourable conditions, ascogonia and antheridia are differentiated after forty to fifty hours. Ascogonia and antheridia may be situated on the same or on more remote branches. They proliferate as short branches perpendicular to the mycelial hyphae and branch dichotomously twice or thrice. The terminal branches of different origin grow together as an ascogonial and an antheridial branch, which coil around each other. There are usually four to eight coils in a cluster formed by a main ascogonial and antheridial branch.

All these elements are multinucleate. A unicellular trichogyne is separated at the top of the ascogonia.

Much difference of opinion exists among cytologists concerning the conduct of the nuclei and the occurrence of a nuclear fusion in the ascogonium (cf. Zukal, 1886; Claussen, 1905; Dangeard, 1903a, b; 1907; Swingle, 1934).

Cells at the base of the gametangia or of adjacent hyphae proliferate and branch repeatedly to form the short-celled hyphae at the base of the fruit body. Several of the hyphae elongate and form the paraphyses. Investing hyphae are not differentiated.

Near their base, the ascogonia proliferate to form ascogenous hyphae. Crozier initials are formed on the ascogenous hyphae which develop into young asci. Meiosis takes place in the ascus and eight ascospores are formed. The asci swell strongly and protrude on ripening. The spores are forcibly discharged.

In *Ascodesmis*, the hymenium and even the ascogonium are exposed from the first until the maturation of the asci. Such fruit bodies are termed eugymnophymenial ascomata (without excipulum) and represent here the most reduced type of development in the Discomycetes.

#### STRUCTURE

A great uniformity consists in the structure of the species of *Ascodesmis*.

The general ultrastructure has been described by Moore (1963, 1965), Carroll (1967), and Brenner & Carroll (1968).

**MYCELIUM.**—The mycelium consists of hyaline, septate, cylindrical hyphae that branch monopodially. No formation of conidia or spermatia has been observed.

**APOTHECIA.**—The apothecia are very simple in structure, consisting only of a bundle of asci surrounded by paraphyses on a small base.

The number of asci in each fruit body is rather variable from two to five in the smallest and up to over thirty in the largest. Often individual apothecia may contain more than a single bundle of ascogonia and antheridia. Most species, under favourable conditions, show a tendency to aggregate on the surface of the substrate and form complexes or crusts. In such complexes it is often difficult to distinguish the individual apothecia.

**ASCI.**—The asci are obovoid to broadly clavate with a broad base and a rounded top. The thin wall and the periascus do not stain blue with iodine.

At maturity, the asci are swelling strongly and proliferating above the hymenial surface when the maximum length of asci is rather variable.

In a very late stage a large operculum is differentiated at the top of the ascus. The position of the operculum is determined by the direction of the maximum light intensity (O'Donnell & al., 1976).

As seen with the electron microscope (van Brummelen, 1978; 1981; O'Donnell & al., 1976; Samuelson, 1978), the operculum is sharply delimited by a weak indentation on the inside where the wall disintegrates circumscissilely within a narrow zone from both sides. The ascostome is smooth. A funnel and a funiculus (respectively 'entonnoir' and 'tractus apical' of Chadefaud) are not differentiated in the top of the ascus, which is in contrast with the asci in most of the other genera of the Pezizales.

**ASCOSPORES.**—The ascospores have the most important characters for the identification of the species.

The shape of the ascospores varies from ellipsoid to perfectly spherical. The mean length/breadth ratio has proved to be a more reliable measure than circumscriptions in words.

Only mature ascospores are measured exclusive of their ornamentation for identification.

Young spores are hyaline and smooth before the formation of an ornamentation. At first, the ornamentation on the surface of the spores is visible as hyaline spines, warts, crests, or reticulations which stain with cotton blue or methyl blue. Brown pigment is gradually formed in these ornamentations. In fully mature ascospores, the ornamentation is pale to dark brown and does not stain any longer with cotton- or methyl blue. Such staining at an intermediate stage of ripening will show spores only partly turning blue. This may explain the blue staining 'perispore', observed in some species of *Ascodesmis* (Obrist, 1961). Sometimes the ascospores were found to be discharged without reaching the full intensity of the brown pigment.

Le Gal (1949) described two different types of origin of the spore ornamentation in *A. microscopica* and *A. nigricans*. However, electron microscopical studies on the same species by Merkus (1973) revealed that the development of the ornamentation is according to the same process for both. A process which proved to be unique among the Pezizales so far studied (Merkus, 1976).

**PARAPHYSES.**—The paraphyses are rather frequent, septate, hyaline, cylindrical, often rather stout, simple or branched at the base. Their ends are scarcely enlarged. Often rather large; colourless vacuoles are seen with rather diffuse lipid contents.

#### HABITAT AND DISTRIBUTION

**HABITAT.**—All known species of *Ascodesmis* are coprophilous. Dung of carnivores is the most common substratum but they also occur on dung of herbivores and omnivores. They have sometimes been isolated from materials such as soil, seeds, and sewage, which are likely to have been contaminated by dung.

DISTRIBUTION.—Since the small size of the apothecia make them unlikely to be collected frequently, it is difficult to draw conclusions about their distribution.

Most collections originate from localities in Europe, Canada, and the United States. Only incidental records are available from Asia, Africa, Australia, and South America. Despite this lack of information, it is possible to conclude that *Ascodesmis nigricans*, *A. microscopica*, and *A. sphaerospora* are cosmopolitan. The latter species is probably more common on the American continent than in Europe.

*Ascodesmis porcina* has a wide distribution but is probably more or less confined to the tropical region.

### ASCODESMIDACEAE Schroet.

Ascodesmidaceae Schroet. in Krypt.-Fl. Schles. 3 (2), 31. 1893 ('Ascodesmidacei'; fam.). — Type: *Ascodesmis* Tiegh.

Ascodesmidoideae Brumm. in Persoonia (Suppl.) 1: 59. 1967. — Type: *Ascodesmis* Tiegh.

Ascodesmidoideae Brumm., emend Korf in Mycologia 64: 949. 1972; Korf in The fungi (ed. Ainsworth & al.) 4A: 270. 1973 (in part).

Ascomata eugymnohymenial, very small. Receptacle restricted to a small group of basal hyphae. Excipulum absent. Asci broad, thin-walled, not staining blue with iodine, without funiculus and funnel. Operculum very large, sharply delimited by a weak indentation at the inside of the ascus where the wall disintegrates circumscissilely within a narrow zone from both sides. Ascospores without oil globules, nonseptate. Secondary wall material at first hyaline, finally brown, forming directly a permanent and rigid ornamentation on the outer surface of the primary wall. Paraphyses present, septate.

Fimicolous.

GENUS.—*Ascodesmis* Tiegh.

EXCLUDED GENERA.—*Pyronema* Carus, *Zukalina* O.K., *Boudiera* Cooke, *Lamprospora* De-Not., *Svrcekia* Kub., *Ascocalathium* Eidam apud Schroet., *Pulparia* P. Karst., *Sphaerozone* Zobel in Corda, *Jafneadelphus* Rifai.

The present concept of the Ascodesmidaceae is mainly based on microscopic and submicroscopic characters of asci and ascospores. It is therefore remarkable that Schroeter's (1893) diagnosis of the family still holds. However, his inclusion of the poorly known genus *Ascocalathium* Eidam apud Schroet. is not tenable. The position of this genus with cylindrical asci, smooth, hyaline ascospores and conspicuous, very long, acuminate, setiform paraphyses is very questionable.

The ascospores of the Ascodesmidaceae—as this family is understood here—are unique among the Pezizales because their ornamentation is immediately constituted by the secondary wall material in a definitive form (Merkus, 1973; 1976). The secondary wall is internally differentiated. The formation of the operculum in the ascus wall is also distinguished as a special type within the Pezizales (van Brummelen, 1978).

The family Ascodesmidaceae remains restricted to the type genus.

Many authors (e.g. van Tiegh, 1876; Saccardo, 1884; Masee, 1895; Masee & Salmon, 1902; Dangeard, 1907; Fennell, 1973; Benny & Kimbrough, 1980) see in *Ascodesmis* a very primitive type of discomycete related to the Gymnoascaceae. Von Arx (1967, 1971) con-

siders it as the most primitive of all Ascomycetes, while others (Le Gal, 1949; Durand, 1969; Nicot & Durand, 1970; Delattre-Durand & Janex-Favre, 1979) support the view of a specialized discomycete which has undergone a strong reduction.

The idea of a relationship with the Gymnoascaceae is based on the simplicity of the ascomata and similarities in gametangiogamy but the asci in *Ascodesmis* are typically operculate.

In view of the complex structure of asci and ascospores, *Ascodesmis* is here considered as a rather specialized organism with a strongly reduced receptacle.

Seaver (1928) placed *Ascodesmis* in his highly artificial tribe Sphaerosporeae of the Pezizales in which he united all genera of operculate Discomycetes with hyaline or brown spherical ascospores. All species of *Ascobolus* sect. *Sphaeridiobolus* (Boud.) Brumm. were placed in the synonymy of *Ascodesmis*.

Korf (1972, 1973) recognized a very extensive family Pyronemataceae with five subfamilies, one of which is the Ascodesmidoidea, characterized by asci that do not stain blue with iodine and ascospores or cell walls with brown pigments. Besides *Ascodesmis*, he includes *Pulparia* P. Karst., *Sphaerozone* Zobel in Corda, and *Jafneadelphus* Rifai.

*Ascodesmis* was considered to be related to *Boudiera* by e.g. Cooke (1877), Le Gal (1949), Obrist (1961), Eckblad (1968), and Kimbrough (1970). The latter genus, however, is characterized by asci clearly staining blue with iodine, an opercular type related to *Ascobolus* and *Saccobolus* (van Brummelen, 1978) and a wholly different development of the spore ornamentation (Merkus, 1974; 1976).

In our (van Brummelen, 1967) monograph of *Ascobolus* and *Saccobolus*, we created a new subfamily Ascodesmidoideae within the Ascobolaceae to accommodate the genus *Ascodesmis* but later research, especially on the fine structure of asci (van Brummelen, 1968) and ascospores (Merkus, 1973; 1976), has convinced us that those fungi are not closely related to *Ascobolus*, *Saccobolus*, or any other genus of Pezizales sufficiently investigated. Their isolated position within the Pezizales is best expressed by the reinstallation of the family Ascodesmidaceae.

### ASCODESMIS Tiegh.

*Ascodesmis* Tiegh. in Bull. Soc. bot. Fr. 23: 275. 1876. — Lectotype: *Ascodesmis nigricans* Tiegh.

Apothecia superficial or immersed, sessile, very small, 50–300 µm diam., consisting of a bundle of asci surrounded by paraphyses on a small subhymenial group of strongly intermingled short-celled hyphae. Excipulum absent. Asci ellipsoid, obovoid, oblong-obovoid or broadly clavate, rounded above, with a broad base or a short broad stalk, thin-walled, protruding at maturity, 8-spored or rarely with only part of the spores developed. Ascospores multiseriate or irregularly disposed in the upper part of the ascus, free, globular, subglobular, or broadly ellipsoid, without oil globules, at first hyaline, becoming brown or brownish at maturity, ornamented with a pattern of spines, warts, ridges, or reticulations. Paraphyses usually frequent, septate, rarely branched, hyaline. Mycelium hyaline, septate, consisting of coenocytic elements, branching monopodially, with ascogonia and antheridia developing as short dichotomously ramifying side branches.

HABITAT.—Fimicolous, also isolated from soil samples.

ETYMOLOGY.—From Greek ἀσχος, leather sack and δεστική, bundle: a bundle of asci.

When van Tieghem (1876) introduced the genus *Ascodesmis* he included two species: *A. nigricans* and *A. aurea*. The former was described in detail and is the object of the author's extensive studies on the development of the fruit body, while *A. aurea* has only a very fragmentary description.

Van Tieghem remarks: 'C'est surtout l'*A. nigricans* que je me suis appliqué à cultiver tant en grand sur crottin de cheval bouilli, qu'en cellule dans divers liquides nutritifs. Aussi est-ce de cette espèce et surtout des résultats obtenus sur elle par les cultures cellulaires qu'il sera exclusivement question dans ce que va suivre!'

Considering these statements of van Tieghem Saccardo's (1884) typification of the genus *Ascodesmis* by *A. aurea* cannot be correct and should not be followed as was done by Eckblad (1968).

It is clear that van Tieghem's knowledge of *Ascodesmis* was almost exclusively based on *A. nigricans* and that only this species can be the lectotype. *Ascodesmis nigricans* was selected as type by Clements & Shear (1931) on other grounds.

#### KEY TO THE SPECIES OF ASCODESMIS

- 1a. Ascospores spherical, subglobose, or broadly ellipsoid; length/breadth ratio under 1.2: ..... 2  
 b. Ascospores broadly ellipsoid to ellipsoid; length/breadth ratio over 1.2: ..... 3  
 2a. Ascospores ornamented with round warts, only rarely with a few connectives or short crests ..... 2. *A. nana*  
 b. Ascospores ornamented with a more or less regular net-work of ridges ... 6. *A. sphaerospora*  
 3a. Ascospores more than 16 µm long ..... 4. *A. macrospora*  
 b. Ascospores less than 16 µm long: ..... 4  
 4a. Ascospores ornamented with an irregular net-work of prominent ridges ... 5. *A. microscopica*  
 b. Ascospores without such a network: ..... 5  
 5a. Ascospores ornamented with isolated or anastomosing spines with only a few connectives; the spines often broadened at their tips ..... 1. *A. nigricans*  
 b. Ascospores ornamented with one very conspicuous simple or branched ridge (up to 3 µm high) extending over the major part of the spore surface, together with isolated or occasionally connected warts and spines ..... 3. *A. porcina*

#### 1. ASCODESMIS NIGRICANS Tiegh.—Fig. 1

*Ascodesmis nigricans* Tiegh. in Bull. Soc. bot. Fr. 23: 275. 1877. — Holotype: not known to be in existence; type locality near Paris, France. Neotype: on dung of goat and sheep (with conserved part of culture), Adiopodoumé, near Abidjan, Ivory Coast, VII. 1949, M. Moreau (PC-A2365).

*Ascodesmis echinulata* Bainier in Bull. Soc. mycol. Fr. 23: 139, pl. 19 fs. 4-7. 1908. — Type: represented by Bainier l.c. pl. 19 fs. 4-7; type locality France.

EXCLUDED.—*Ascodesmis nigricans* Tiegh. sensu Schroeter in Kryptog.-Fl. Schles. (ed. Cohn) 3(2): 32. 1883 = *Ascodesmis microscopica*.

*Ascodesmis nigricans* Tiegh. sensu Massee, Brit. Fungus-Fl. 4: 19. 1895 = *Ascodesmis microscopica*.

*Ascodesmis nigricans* Tiegh. sensu Saccardo, Syll. Fung. 8: 825. 1889 = *Ascodesmis microscopica*.

*Ascodesmis nigricans* Tiegh. sensu Swingle in Am. J. Bot. 21: 519-545. 1934 = *Ascodesmis sphaerospora*.

Apothecia solitary or gregarious, rarely confluent, superficial or immersed, sessile on a narrow base, 70-200(-250) µm diam., up to 100 µm high, at first subcylindrical, obconical, or

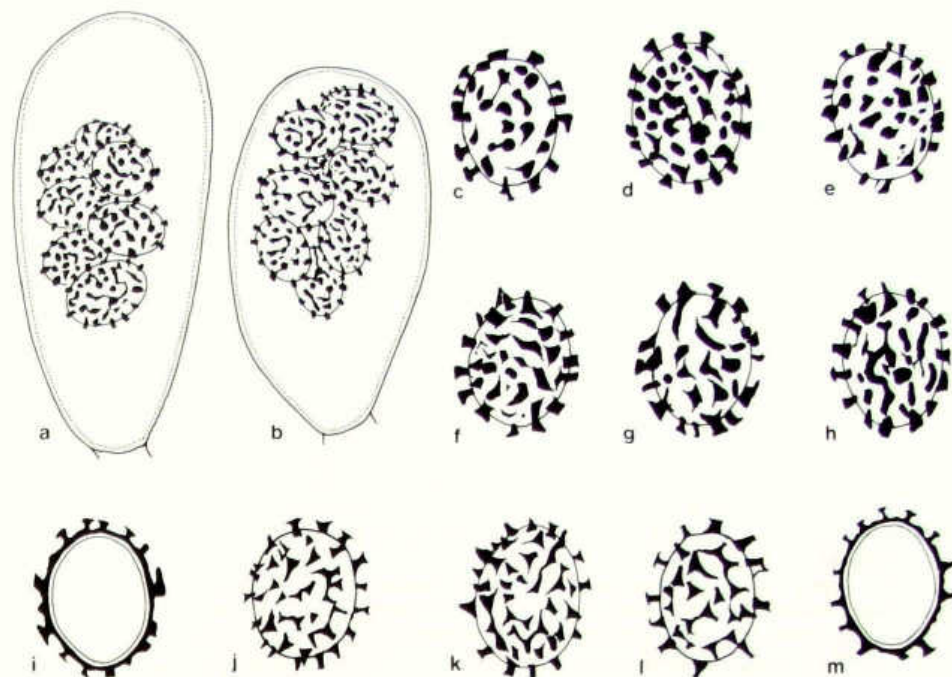


Fig. 1. *Ascodesmis nigricans*. — a, b. Asci × 1000. — c-h, j-l. Ascospores × 1600. — i, m. Ascospores in optical section × 1600. (a-i from Bartlett, 4.XII.1979, L; j-m from neotype of *A. nigricans*, PC-A2365.)

barrel-shaped, becoming flattened with age, hyaline than brown, consisting of 3-10(-20) asci surrounded by paraphyses. Hymenium convex, dotted with the brown protruding tips of ripe asci. Hypothecium scarcely differentiated, of strongly intermingled thin-walled hyphae 4-8 µm wide. Excipulum absent. Asci broadly clavate to obovate with a broad base or a short broad stalk, rounded above, with a very large operculum, 45-55(-65) × 25-30 µm, 8-spored. Ascospores irregularly arranged in the upper part of the ascus, broadly ellipsoid to ellipsoid (length/breadth ratio 1.2-1.5, average 1.25-1.35), at first hyaline, soon becoming chocolate brown, (9.5-)10.5-12.0(-12.5) × (7.5-)8.5-9.5(-10) µm (without ornamentation), without oil globules or granules, ornamented with isolated or rarely anastomosing spines, with a few fine connectives; the spines usually flat and broadened at their tips. Paraphyses rather frequent, septate irregularly cylindrical, simple or branched at the base, hyaline, 3-5.5 µm thick, not or scarcely enlarged at the tip, not embedded in mucus, containing vacuoles and granules. Mycelium hyaline, cylindrical, sometimes in part aerial, without conidia or spermatia. Antheridia and ascogonia with broad symmetrically dichotomous branches.

HABITAT.—On dung of dog, fox, rat, pig, sheep, goat, donkey, and ostrich, also isolated from soil and beans.

ETOMOLOGY.—From Latin *nigricans*, becoming black.

ILLUSTRATIONS.—Van Brummelen in Persoonia 10: 118 f. 9. 1978 (E.M.); van Brummelen in Ascomycete Systematics (ed. Reynolds), Chapt. 3: 34 f. 3.9. 1981 (E.M.); Le Gal in Revue Mycol. 14: 87-90 fs. 1-3. 1949; Merkus in Persoonia 7: pls. 28 A, B, 31, 33, 37, 38. 1973 (E.M.); Oubris in Can. J. Bot. 54: 573-575 fs. 3, 4, 9, 10. 1975 (development, S.E.M.).

MATERIAL EXAMINED.—FINLAND: on dog dung, Åbo (Turku), 6.X.1861, *Karsten* (H-A2745).

GREAT BRITAIN: culture, Edinburgh, Scotland, *s. dat.*, *Richardson* (L); culture isolated from goat dung, Univ. Cardiff, 4.XII.1979, *Bartlett* (L); on dung of ostrich, Zoological Garden, Kew, VI.1901 [Masse & Salmon] (K).

THE NETHERLANDS: culture isolated from sandy soil, Wageningen, V.1968, *Tigelaar* (CBS 389.68).

DENMARK: on album graecum, *s. loc.*, 18.VII.1874, *E. C. Hansen* (C-A59); on dog dung, Hellebäck, VII.1874, *E. C. Hansen* (K-A2515).

FRANCE: culture, *s. loc.*, *s. dat.* (Mycothèque PC No. 315, L).

LIBYA: on dung of goat (comm. Dr. H. O. Sleumer), near Tripoli, 9.VIII.1971, *van Brummelen* 3296 (L, also culture).

IVORY COAST: on dung of goat and sheep, with conserved part of culture, Adiopodoumé near Abidjan, VII.1949, *M. Moreau* (PC-A2365, as *A. nigricans* det. Le Gal, neotype of *A. nigricans* Tiegh.); culture, idem, VIII.1949, *M. Moreau* (Mycothèque PC No. 100; CBS 114.53).

PAKISTAN: on donkey dung (comm. T. Wassif), Karachi, XII.1962, *Cain* (TRTC 38847).

INDIA: culture isolated from dung, Sargar, *s. dat.*, *S. C. Agrawal* A17 (CBS 163.74; IMI 179.865).

INDONESIA: on rat dung, Bogor, III.1956, *Boedijn* (drawing, L).

CANADA: on dog dung (?), Bear Island, Lake Timagami, Ontario, 15.VIII.1931, *Cain* (TRTC 34711); on fox dung, Nashville, York Co., Ontario, 4.II.1957, *Cain* (TRTC 32679); on dog dung, Nashville, York Co., Ontario, 5.XII.1959, *Cain* (TRTC 35292); isolated from soil, Nashville, York Co., Ontario, XI.1963, *Cain* (TRTC 40454); isolated from beans, Guelph, Ontario, 24.XI.1948, *J. W. Groves* 20239 (DOAM).

U. S. A.: on dog dung, Cambridge, Massachusetts, II.1887, *Thaxter* (FH-A3156 in part); grown on agar, *s. loc.*, New York, *s. dat.*, *B. O. Dodge* 31-1 (NY-A1065; TRTC-B2001); on pig dung, New Jersey, 11.XII.1915, *Seaver* (NY-A1085 in part); on dung of carnivorous animal, Colfax, Louisiana, 25.VIII.1960, *Cain* (TRTC 36466).

When van Tieghem (1876) founded the genus *Ascodesmis*, he gave a rather diffuse description of *A. nigricans*, which was the subject of his detailed developmental studies.

The following parts of his description are relevant: '... le fruit mûr de ces plantes se compose simplement d'un bouquet ou d'une rosette d'asques divergents, entremêlés de paraphyses, le tout inséré à la surface supérieure d'une petite masse cellulaire arrondie, qui à son tour s'attache au milieu de sa face inférieure et par un court rameau à un filament mycélien. Complètement dépourvus d'enveloppe ou de périasque, ces fruits sont très-petits, le plus gros atteignant à peine 2 à 3 dixièmes de millimètre; ... Les asques, ovales allongés ou claviformes, contiennent huit spores bisériées qu'ils mettent tardivement en liberté par résorption ou déchisure de leur membrane mince et incolore. Les spores, sphériques ou subsphériques, dont le protoplasme est homogène et incolore, sont revêtues d'une exospore colorée et cuticularisée, munie de remarquables épaississements. ... Dans l'*A. nigricans*, où la spore légèrement ovale mesure 0<sub>mm</sub>, 012 sur 0<sub>mm</sub>, 010, ce ne sont aussi d'abord que des pointes brunes, plus foncées que le reste de la membrane, et parfois même la chose paraît en rester là; mais le plus souvent l'exospore se développe bientôt au-dessous des pointes en les soulevant et forme un réseau brun à mailles hexagonales ou pentagonales qui porte une pointe à chacun de ses sommets, ...'

Since no illustrations are given, nor have any specimens of van Tieghem been preserved, *A. nigricans* should be interpreted from the original description.

Madame Le Gal (1949) succeeded very well in identifying van Tieghem's fungus with living material sent by M. Moreau from Abidjan (Ivory Coast). The development of the ascospore ornamentation agrees especially well.

We agree with Obrist (1961: 948) that Le Gal's specimen should be designated as the neotype of the species. This, however, is the preserved part of the culture studied by Le Gal (*M. Moreau*, VII. 1949, PC-A2365). The indication of Culture No. 100 of the 'Mycothèque' of the Laboratoire de Cryptogamie in Paris as neotype (Obrist, l.c.: 947) is not allowed according to Article 9.5 of the present International Code of Botanical Nomenclature.

*Ascodesmis echinulata* Bainier with ascospores about 11 × 8.4 µm and isolated spines, without connectives, fits well within the variability of *A. nigricans* and is considered to be a synonym.

The present species can be distinguished from *A. microscopica* by the smaller ascospores and the usually isolated spines of the spore ornamentation. It differs from *A. nana* in the longer ascospores and spines that are often flattened and broadened at the ends.

*Ascodesmis nigricans* is also recorded from Kenya (Minoura, 1969) and Taiwan (Liou & Chen, 1977). It is a cosmopolitan species.

## 2. *Ascodesmis nana* Brumm., *sp. nov.*—Fig. 2

Apothecia solitaria aut gregaria, 60–100 µm diam., 60–70 µm alta, initio subcylindracea vel doliiformia, deinde semiglobularia, constans ex 4–9 ascis et paucis paraphysibus. Excipulum deest. Asci obovoidei ad ellipsoidei, 50–639–80) × 25–28 µm, 8-spori. Ascosporeae globulosae, globosae ad late ellipsoideae, initio hyalinae, deinde pallide brunneae, 8.5–10.0(–11.0) × 8.3–9.5(–10.0) µm, verucis rotundatis satis magnis aut parvis ornatae, aliquando connectivis tennibus aut cristis brevibus. Paraphyses raeae, septatae, irregulariter cylindraceae. In fimo Pecary tajaou invenitur. Typus: *van Brummelen* 717 (L).

Apothecia solitary or gregarious, superficial or partly immersed, sessile on a rather broad base, 60–100 µm diam., 60–70 µm high, at first subcylindrical or barrel-shaped, then semiglobular and spreading, hyaline then pale brownish, consisting of a bundle of 4–9 asci surrounded by a few paraphyses. Hymenium convex, dotted with the brownish ends of protruding ripe asci. Hypothecium scarcely developed and of only a few thin-walled strongly intermingled short-celled hyphae, 4.5–7.5 µm wide. Excipulum absent. Asci obovoid to ellipsoid, with a short broad stalk, rounded at the apex, with a very large operculum, 50–63(–80) × 25–28 µm, 8-spored. Ascospores irregularly arranged in the upper half of the ascus, globular, globose, or broadly ellipsoid (length/breadth ratio 1.00–1.20, average 1.13), at first hyaline then pale brown, 8.5–10.0(–11.0) × 8.3–9.5(–10.0) µm (excluding ornamentation), without oil globules or granules, ornamented with rather large and small isolated round warts and occasional fine connectives or short crests. Paraphyses rather scarce, septate, irregularly cylindrical, simple, hyaline, 3.5–5 µm thick, not enlarged at the ends, embedded at their base in hyaline or pale brown mucus, containing one or only a few large vacuoles with a lipid substance. Mycelium hyaline, cylindrical, branching monopodially, without conidia or pycnidia.

HABITAT.—Only known from dung of collared peccary.

ETYMOLOGY.—From Latin nanus, a dwarf, staying low.

SPECIMEN EXAMINED.—THE NETHERLANDS: on dung of collared peccary (*Pecary tajaou*), Zoological Garden, Amsterdam, 11.VIII. 1959, *van Brummelen* 717 (type of *Ascodesmis nana*, L; also isolated in culture).

This new species is closely related to *A. nigricans* with which it has in common the presence of small asci and ascospores, also a spore ornamentation consisting mainly of isolated elements.

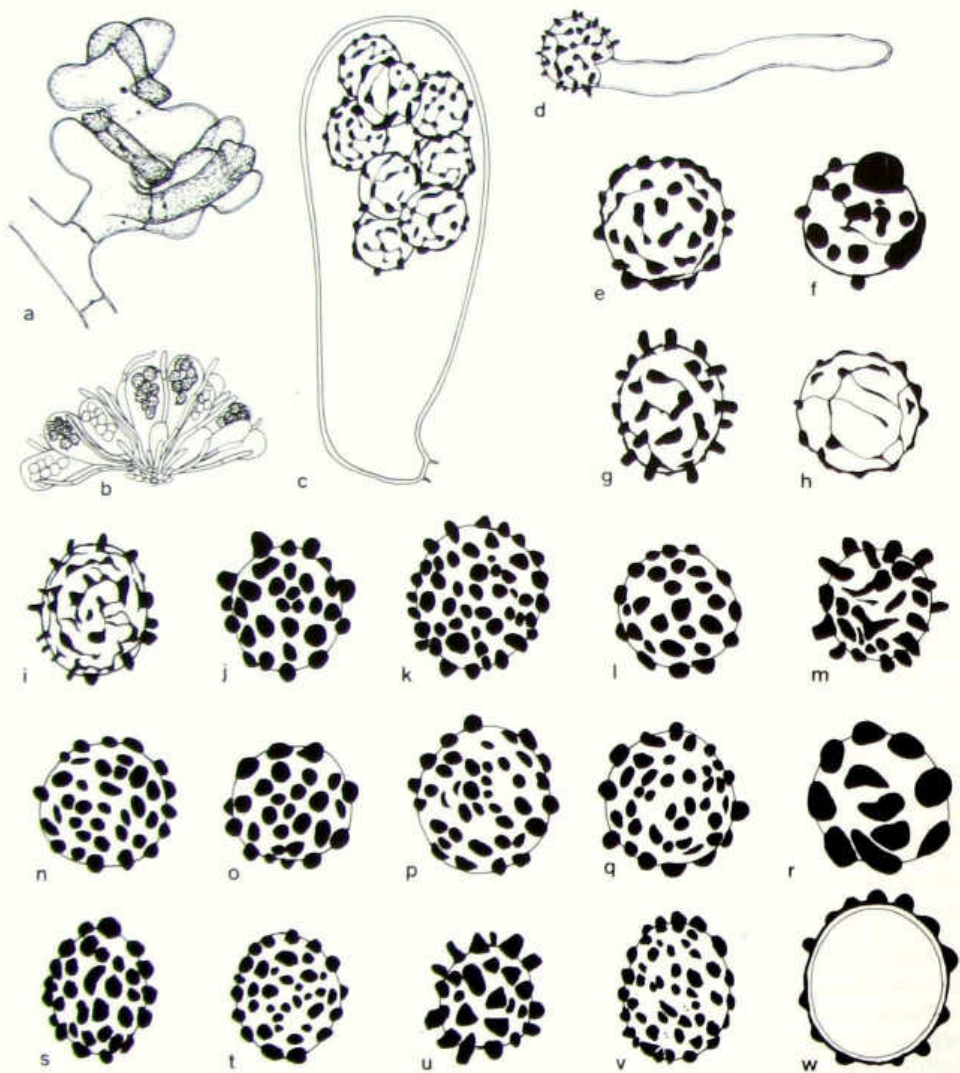


Fig. 2. *Ascodesmia nana*. —a. Gametangia  $\times 1000$ . —b. Apothecium  $\times 125$ . —c. Ascus  $\times 900$ . —d. Germinating ascospore  $\times 900$ . —e–v. Ascospores  $\times 1600$ . —w. Ascospore in optical section  $\times 1600$ . (From type of *A. nana*.)

The ascospores in *A. nana* are subglobular or spherical with a mean length/breadth ratio under 1.15 and isolated round warts. In *A. nigricans* the shape of the ascospores is clearly ellipsoid with a mean length/breadth ratio over 1.2 and isolated or somewhat anastomosing spines, often flattened and broadened at their ends.

### 3. ASCODESMIS PORCINA Seaver—Fig. 3

*Ascodesmia porcina* Seaver in *Mycologia* 8: 3, pl. 172 fs. 6–9, 1916; North Am. Cup-fungi (Operc.) 80, pl. 5 fs. 6–9, 1928. —Holotype: on pig dung [comm. G. L. Fawcett], Porto Rico, I. 1915, Seaver (slides, NY-A1084).

Apotheca solitary or gregarious, superficial, sessile 60–150  $\mu\text{m}$  diam., 80–100  $\mu\text{m}$  high, at first subglobular, then hemispherical, becoming more flattened, finally more or less discoid to pulvinate, hyaline then brown. Hymenium convex, roughened by the protruding brown tips of ripe asci. Hypothecium scarcely differentiated consisting of a few strongly intermingled thin-walled hyphae 4–7  $\mu\text{m}$  wide. Excipulum absent. Asci broadly clavate, oblong, or obovoid, with a broad base or a short broad stalk, rounded above, with a large operculum, 65–80(–90)  $\times$  20–30(–35)  $\mu\text{m}$ , 8-spored. Ascospores irregularly disposed in the upper part of the ascus, broadly ellipsoid to ellipsoid (length/breadth ratio 1.2–1.7, average 1.3–1.55), at first hyaline, then brown, (11.0–)11.5–13.5(–14.5)  $\times$  (7.0–)7.5–10.0(–11.5)  $\mu\text{m}$  (without ornamentation), without oil globules or granules, ornamented with a very variable pattern of isolated warts and spines with occasional fine connectives and with one very conspicuous simple or branched ridge up to 3  $\mu\text{m}$  high extending over the major part of the spore surface. Paraphyses rather scarce, septate, irregularly cylindrical, simple, hyaline, 4–6  $\mu\text{m}$  thick, scarcely enlarged upwards, not embedded in mucus, containing several vacuoles and granules. A conidial state is unknown.

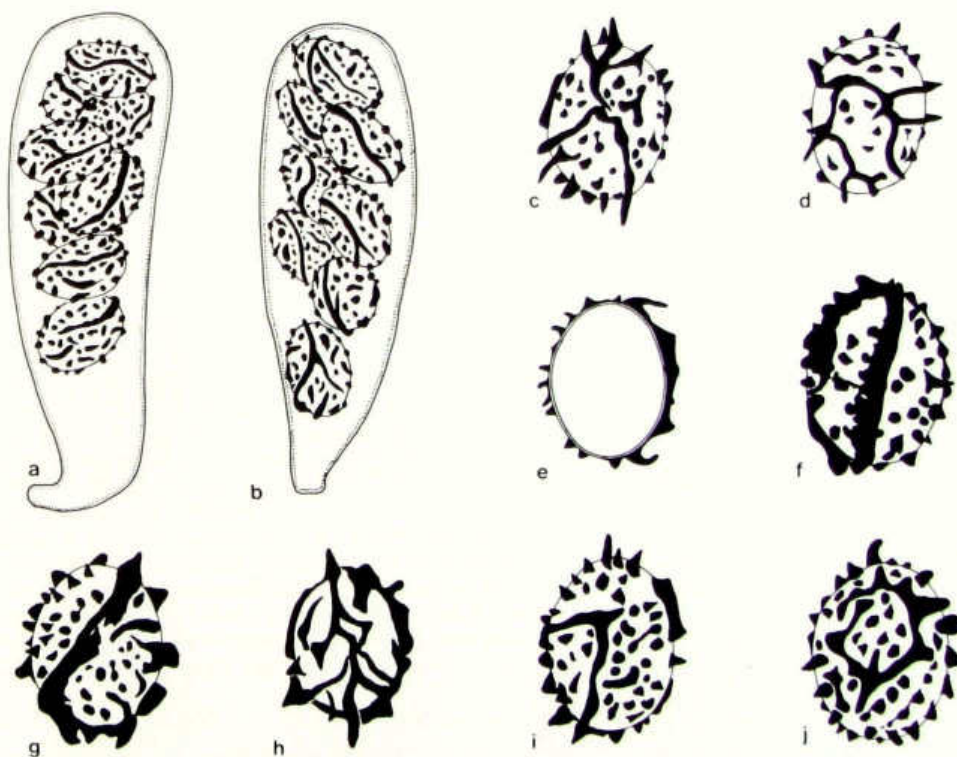


Fig. 3. *Ascodesmia porcina*. —a, b. Asci  $\times 1000$ . —c, d, f–j. Ascospores  $\times 1600$ . —e. Ascospore in optical section  $\times 1600$ . (a, b redrawn after Boedijn, III, 1956, L-B2035; c–j from holotype of *A. porcina*.)

HABITAT.—On dung of rat, peccary, pig, goat, and donkey.

ETYMOLOGY.—From Latin porcinus, a pig; from the habitat of type specimen on pig dung.

ILLUSTRATIONS.—Obrist in Can. J. Bot. 39: 952 f. 11, 1961; Seaver in Mycologia 8: pl. 172 fs. 6–9, 1916. Seaver, North Am. Cup-fungi (Operc.) pl. 5 fs. 6–9, 1928.

MATERIAL EXAMINED.—INDONESIA: on rat dung, Bogor, III, 1956, Boedijn (drawing, L).

NEW GUINEA (West): on goat dung (Comm. Dr. H. O. Seumer), Tablasoefoe, 21. VIII. 1061, van Brummelen 1487 (L).

U. S. A.: on pig dung, New Jersey, 11. XII. 1915 [Seaver] (TRTC-B2003, in part); *s. loc.*, *s. dat.*, Seaver 'No. 4' (slide, NY-A1073).

PORTO RICO: on pig dung [comm. G. L. Fawcett], *s. loc.*, I, 1915, Seaver (slides, NY-A1084, holotype of *A. porcina*).

VENEZUELA: on pig dung, Margarita, 1903, Blakeslee (as *Saccobolus*, FH-A3064); on goat dung, between Manacal and Los Pacitos, NW. of Irapa, Edo. Sucre, 13. VII. 1972, Dumont VE 4892a (TRTC), on dung of burro (donkey), 19 km SW. of Caripe, Edo. Monagras, 19. VII. 1972, Dumont VE 5521r (TRTC).

BRAZIL: on peccary dung (comm. Dr. A. C. Batista), Recife, VIII. 1960, Obrist (TRTC 36308).

This species shows some similarity to *Ascodesmis nigricans* but differs in having ascospores with a conspicuous simple or branched ridge extending over the greater part of the spore surface.

The species is also recorded from Panama (Meyer & Meyer, 1949) and Taiwan (Liou & Chen, 1977). Gunnell's (1960) record for Britain probably relates to another species because of the ascospore characters given.

With the exception of Seaver's specimens grown on pig dung from New Jersey, U.S.A., *A. porcina* shows a circum-tropical distribution.

#### 4. ASCODESMIS MACROSPORA Obrist—Fig. 4

*Ascodesmis macrospora* Obrist in Can. J. Bot. 39: 951 f. 12, 1961. — Type on dung of puma (*Felis concolor*) comm. Dr. A. C. Batista, Recife, Brazil, isolated [by Obrist] I, 1960 (TRTC 35512).

Apothecia solitary or gregarious, often confluent, superficial or semi-immersed, sessile, (100–)140–300  $\mu$ m diam., (100–)120–180  $\mu$ m high, at first hemispherical to subglobular, then often aggregating into a crest, hyaline, finally brown, consisting of a bundle of 8–25 asci surrounded by paraphyses. Hymenial surface convex, roughened by the far protruding ends of ripe asci. Hypothecium scarcely differentiated, consisting of a small group of rounded thin-walled cells 4.5–11  $\mu$ m wide. Excipulum absent. Asci very broadly clavate, oblong, ellipsoid, or obovoid, with a broad base, rounded above 84–115(–150)  $\times$  (29–)35–42  $\mu$ m, 8-spored but sometimes with only a part of the spores developed. Ascospores irregularly disposed in the upper part of the ascus, broadly ellipsoid (length/breadth ratio 1.17–1.30, rarely 1.4), at first hyaline, then brown, (18.0–)19.0–20.5(–21.5)  $\times$  (13.5–)15.0–16.5(–17.6)  $\mu$ m (excluding ornamentation), without oil globules or granules, ornamented with a more or less incomplete irregular network of major ridges and crests 1.5–3.0  $\mu$ m high with smaller and

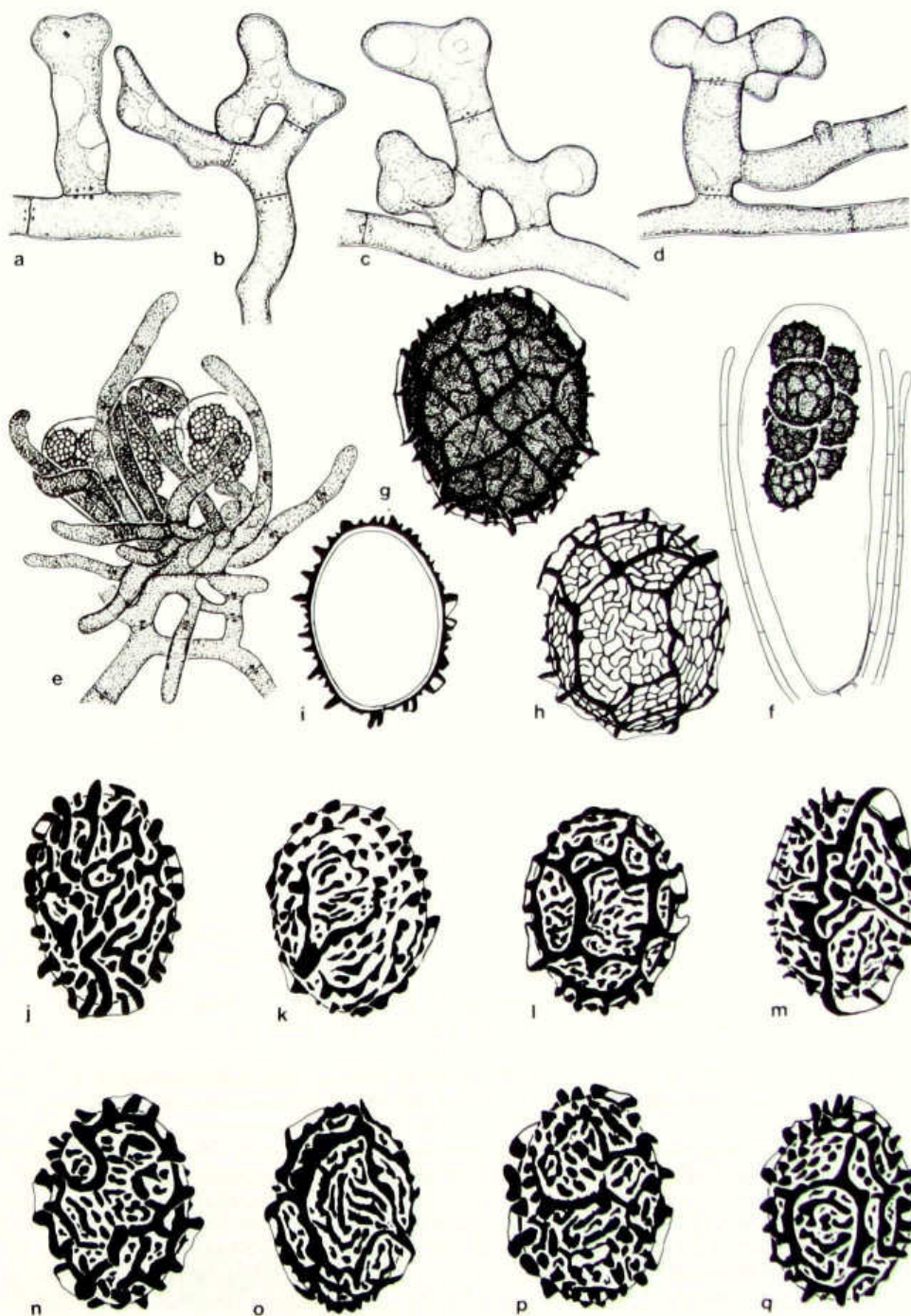


Fig. 4. *Ascodesmis macrospora*. — a–d. Gametangia  $\times$  1000. — e. Apothecium  $\times$  320. — f. Ascus and paraphyses  $\times$  500. — g, h, j, k, l, m, n, o, p, q. Ascospores  $\times$  1600. — i. Ascospore in optical section  $\times$  1600. (a–h from van Brummelen 716; i–q from holotype of *A. macrospora*.)



more delicate ridges and spines up to 1.5  $\mu\text{m}$  high in the space between the meshes. Paraphyses present, septate cylindrical, rarely branched, hyaline, 3–6  $\mu\text{m}$  thick, scarcely enlarged at the tip, not embedded in mucus, contents rather homogeneous. Mycelium hyaline, branching monopodially, without conidia or spermatia.

HABITAT.—On dung of crocodile, puma, and *Cerdocyon thous*.

ETYMOLOGY.—From Greek μακροζ, long (improperly used for μεγαζ, large) and σπορα, a seed; with long spores.

ILLUSTRATION.—Obrist in Can. J. Bot. 39: 952 f. 12, 1961.

MATERIAL EXAMINED.—THE NETHERLANDS: on dung of crocodile, Zoological Garden, Amsterdam, 8.VIII.1959, van Brummelen 716 (L, also as culture 59.19); idem, 13.III.1970, van Brummelen 2749 (L, also as culture 72); idem, 20.IV.1970 (L); idem, 12.V.1970, van Brummelen 2775 (L); idem, 14.XII.1970, van Brummelen 3254 (L).

BRAZIL: on dung of puma (*Felis concolor*) (comm. Dr. A. C. Batista), Recife, isolated [by Obrist] 1.1960 (holotype of *A. macrospora*, TRTC 35512); on dung of *Cerdocyon thous* (comm. Dr. A. C. Batista), Recife, isolated [by Obrist], III.1960 (TRTC 35596).

The present species would appear rather close to *A. microscopica*, differing mainly in the much larger ascospores.

A rather aberrant collection (TRTC 35537), cultivated on Jaguar dung from Brazil, was specially mentioned by Obrist (1961: fig. 1) and included in *A. macrospora*. This fungus has smaller, more broadly ellipsoid ascospores, measuring 14.3–15.5  $\times$  11.5  $\times$  12.7  $\mu\text{m}$ , ornamented with an irregular network. It should not be included in *A. macrospora*, until more is known about the variability of this species.

*Ascodesmis macrospora* seems to be restricted to dung of carnivores. In culture it grows fast and produces mature ascospores within four days after inoculation. Ascospores that have been preserved dry for more than ten years germinated with only a minor delay.

##### 5. ASCODESMIS MICROSCOPICA (Crouan) Seaver—Fig. 5

*Ascobolus microscopicus* Crouan in Anns Sci. nat. (Bot.) IV 7: 175 pl. 4E fs. 20–23, 1857; not *Ascobolus microscopicus* (Wallr.) Sacc., Syll. Fung. 8: 524, 1889. — *Boudiera microscopica* (Crouan) Cooke in Grevillea 6: 76, 1877. — *Ascodesmis microscopica* (Crouan) Seaver in Mycologia 8: 3, 1916 (misapplied). — Type: on album graecum, near Brest, Finistère, France, s. dat., Crouan (PC-A2351).

*Boudiera clausenii* P. Henn. in Hedwigia 42 (Beibl.) 182, 1903. — Type distribution: Rehm, Ascom. 1526.

*Ascodesmis reticulata* Bainier in Bull. Soc. mycol. Fr. 23: 137 pl. 19 fs. 1–3, 1908. — Type: not known to be in existence, represented by Bainier l.c.; type locality, near Paris, France.

EXCLUDED.—*Ascodesmis microscopica* (Crouan) Seaver sensu Seaver in Mycologia 8: 3, pl. 72 fs. 1–5, 1916; North Am. Cup-fungi (Operc.) 79, 1928 = *Ascodesmis sphaerospora* Obrist.

Apothecia solitary, gregarious, or confluent, superficial, sessile (50–)80–200(–250)  $\mu\text{m}$  diam., 70–150  $\mu\text{m}$  high, at first irregularly cylindrical, then obconical and/or flattened, hyaline, finally brown, consisting of a bundle of only a very few asci surrounded by paraphyses. Hymenial surface convex, dotted with the brown protruding tips of ripe asci. Hypothecium scarcely differentiated, of only a few thin-walled, short-celled hyphae 5.5–9.5  $\mu\text{m}$  wide. Excipulum absent. Asci broadly clavate to obovoid, with a broad base, rounded above, with a very large operculum, (63–)70–80(–88)  $\times$  (26–)29–31(–33)  $\mu\text{m}$ , 8-spored. Asco-

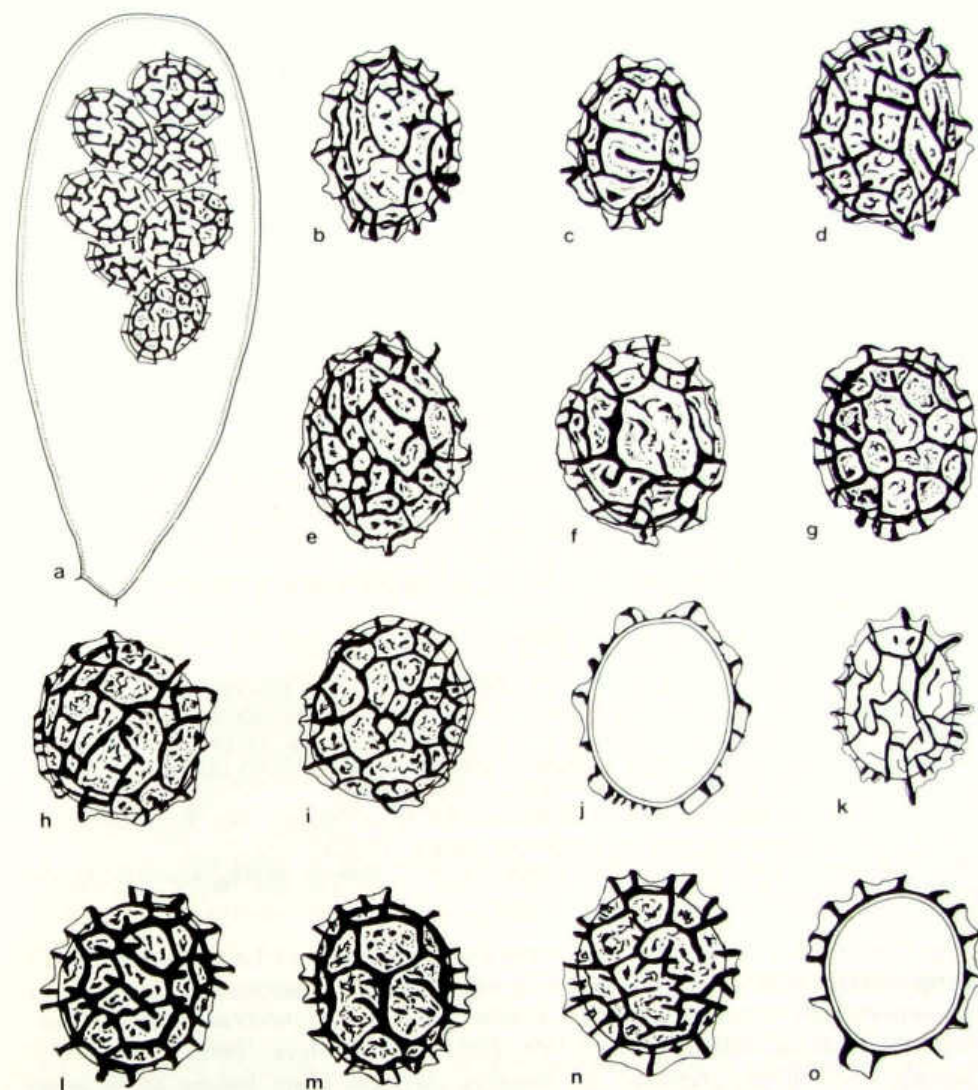


Fig. 5. *Ascodesmis microscopica*. — a. Ascus  $\times$  1000. — b–i, k–n. Ascospores  $\times$  1600. — j, o. Ascospores in optical section  $\times$  1600. (a from G. Arnold m 424, CBS; b–j from type of *A. microscopica*; k–o from Rehm, Ascomyceten 1526, k from M, l–o from S.)

spores irregularly disposed in the upper part of the ascus, broadly ellipsoid, rounded at each end (length/breadth ratio 1.14–)1.20–1.35(–1.50), at first hyaline becoming brown at maturity (11.0–)11.5–14.0(–15.5)  $\times$  (8.0–)9.0–12.0(–13.5)  $\mu\text{m}$  (excluding ornamentation), without oil globules or granules, ornamented with an irregular wide-meshed network of brown ridges up to 2  $\mu\text{m}$  high with enforced points of interception and the spaces within filled with isolated spines, warts or short ridges. Paraphyses frequent, septate, subcylindrical, simple or

branched near the base, hyaline, 4–6 µm thick, not or scarcely enlarged at the tip, not embedded in mucus, containing a few large vacuoles with lipoids. Mycelium hyaline, cylindrical, branching monopodially, without conidia or spermatia.

HABITAT.—On dung of dog, wolf, rabbit, goat, rat, and *Cerdocyon thous*.

ETYMOLOGY.—From Greek μικρός, small and σκοπεῖν, to observe, to examine; so minute as to be invisible without the use of a microscope.

ILLUSTRATIONS.—van Brummelen in *Persoonia* 10: 118 f. 10. 1978 (E.M.); van Brummelen in *Ascomycete Systematics* (ed. Reynolds). Chapt. 3: 34 f. 3. 10. 1981 (E.M.); Claussen in *Bot. Ztg.* 63: pls. 1–3. 1905 (very good, as *Boudiera*); Crouan in *Annls Sci. nat. (Bot.)* IV 7: pl. 4E fs. 20–23. 1857 (not very characteristic, as *Ascobolus microscopicus*); Hennings in *Hedwigia* 42 (Beibl.): (182) fs. I–III. 1903 (as *Boudiera clausenii*); Le Gal in *Revue Mycol.* 14: 95 f. 4. 1949; Merkus in *Persoonia* 7: pls. 28c, 29, 30, 32, 34–36. 1973 (E.M.).

MATERIAL EXAMINED.—GREAT BRITAIN: culture, Edinburgh, Scotland, *s. dat.*, Richardson *s.n.* (L).

FRANCE: on dog dung, Bois de Boulogne [near Paris], VII.1901, Rolland (FH–A3079); idem, VIII.1901 (PC–A2247).

GERMAN FEDERAL REPUBLIC: on dung of rabbit and cultured, Freiburg, Baden, *s. dat.*, Claussen (comm. P. Hennings), in Rehm, *Ascom.* 1526 (type distribution of *Boudiera clausenii*); BPI, HBG; K, M, MPU, PAD, S, W, ZT); idem, VIII.1903, Claussen, in Sydow, *Mycoth. germ.* 132 (*Boudiera clausenii*); BPI, E, K, M, MPU, S, U, W, ZT).

GERMAN DEMOCRATIC REPUBLIC: culture isolated from dung, 'Wilder Graben', Weimar, 20.V.1975, G. Arnold *m* 424 (CBS).

LIBYA: on goat dung (Comm. Dr. H. O. Sleumer), near Tripoli, 3.VIII.1971, van Brummelen 3292 (L); idem, 9.VIII.1971, van Brummelen 3297 (L).

CANADA: on dog dung, Nashville, York Co., Ontario, 12.XII. 1959, Cain (TRTC 35293); on wolf dung, Shabotic River, Algoma District, Ontario, 20.VI.1961, Cain (TRTC 38512).

U. S. A.: culture isolated from rat dung, Los Angeles Co., California, IV.1961, Orr 0–523 (CBS 124.61); on dog dung, Cambridge, Massachusetts, *s. dat.*, Thaxter (FH–A3152); idem (FH–A3154); on dog dung, New Haven, Connecticut, *s. dat.*, Thaxter (FH–A3155).

VENEZUELA: on dog dung, N. of Maraval, along Rio Aguas Calientes, Edo. Sucre, 8.VII.1972, Dumont VE 4338b (ascospores only; as *Ascodesmis caninus*, TRTC).

BRAZIL: on dung of *Cerdocyon thous* (comm. Dr. A. C. Batista), Recife, isolated [by Obrist] III.1960. (TRTC 35597).

The name of this species has been variously misapplied until Le Gal (1949) gave a description of the type specimen. In general *A. microscopica* was confused with *A. nigricans* by European authors (Saccardo, 1889; Schroeter, 1893; Masee, 1895) and with *A. sphaerospora* by American authors (Seaver, 1916, 1928; Meyer & Meyer, 1949).

Cavara (1905) already presumed that *Boudiera clausenii* Henn. belongs to the genus *Ascodesmis*. This is confirmed by a study of the type material. Henning's name is a synonym of *A. microscopica*.

*Ascodesmis reticulata* Bainier (1908) with ascospores measuring 15 × 11 µm and a brown or blackish net-work is certainly a synonym of *A. microscopica*.

The present species was apparently not known to Obrist (1961), who did not report any collection and referred to Le Gal's (1949) description. Some of the collections which he included in *A. sphaerospora* proved to be typical representatives of *A. microscopica*. Both are certainly closely related but can be maintained as separate taxa at the specific level.

The ascospores in *A. microscopica* are more ellipsoid with a mean length/breadth ratio

over 1.2 while the net-work of the ornamentation is rather irregular and often incomplete. In *A. sphaerospora* the shape of the ascospores is subglobular, rarely perfectly spherical, with a mean length/breadth ratio under 1.15, while the net-work of the ornamentation is more regular and complete.

*Ascodesmis microscopica*, which is also recorded from Taiwan (Liou & Chen, 1977), is a cosmopolitan species.

## 6. ASCODESMIS SPHAEROSPORA Obrist—Fig. 6

*Ascodesmis microscopica* (Crouan) Seaver sensu Seaver in *Mycologia* 8: 3, pl. 72 fs. 1–5. 1916 (non sensu Crouan). — *Ascodesmis sphaerospora* Obrist in *Can. J. Bot.* 39: 948. 1961 (nomen novum). — Type: on dung of raccoon dog, Bronx Zoological Garden, New York, U.S.A., XI.1915, Seaver (NY–A1066).

Apothecia solitary or gregarious, often confluent, superficial or partly immersed, sessile, (80–)110–230 µm diam., 90–120 µm high, at first hyaline becoming brownish with maturity, obconical, then semiglobular and more flattened, consisting of a bundle of 5–20(–50) asci surrounded by paraphyses. Hymenium convex dotted by the brown ends of protruding ripe asci. Hypothecium scarcely differentiated, consisting of a few strongly intermingled thin-walled, short-celled hyphae, (5–)7–9 µm wide. Excipulum absent. Asci cylindrical-clavate or oblong, with a broad often curved stalk, rounded above, with a very large operculum 15–20 µm wide, (60–)70–95(–100) × (26–)29–33(–34) µm, 8-spored. Ascospores irregularly arranged, globular, subglobose to broadly ellipsoid (length/breadth ratio (1.05–)1.10–1.20(–1.26), average (1.05–1.15) at first hyaline, brown at maturity, (10.5–)11.5–13.0(–14.0) × (9.0–)10.0–11.5(–12.0) µm (without ornamentation), without oil globules or granules; ornamented with a more or less regular net-work of ridges and more prominent spines (up to 1.8 µm high) at the points of interception and the spaces within filled with isolated spines and short ridges. Paraphyses rather frequent, septate, cylindrical, simple or branched at the base, hyaline, 2.7–4.8 µm thick, enlarged up to 6.0 µm at the tip, not embedded in mucus, vacuoles with lipid substance and granules. Mycelium hyaline, cylindrical, branching monopodially, without conidia or spermatia.

HABITAT.—On dung of lion, tiger, jaguar, American ocelot, *Cerdocyon thous*, dog, raccoon-dog, rabbit, elk, and giraffe, also isolated from soil and from a trickling-filter.

ETYMOLOGY.—From Greek σφαῖρα, a ball, a globe and σπορά, a seed; with spherical spores.

ILLUSTRATIONS.—Brenner & Carroll in *J. Bact.* 95: 660–669 fs. 1–44. 1968 (E.M.); Delattre-Durand & Janex-Favre in *Bull. Soc. mycol. Fr.* 95: 53–59 pls. 1–4. 1979 (development, as *A. microscopica*); Moore in *Nova Hedwigia* 5: pls. 38–43. 1963 (E.M.); Obrist in *Can. J. Bot.* 39: 949 fs. 2–9. 1961; O'Donnell & al. in *Can. J. Bot.* 54: 573–576 fs. 1, 2, 5–8, 11–14. 1975 (development, S.E.M.); Samuelson in *Am. J. Bot.* 65: 752 fs. 9–16. 1978 (E.M.); Seaver in *Mycologia* 8: pl. 172 fs. 1–5. 1916 (as *A. microscopica*); Seaver, *North Am. Cup-fungi (Operc.)* pl. 5 fs. 1–5. 1928 (as *A. microscopica*); Swingle in *Am. J. Bot.* 21: pls. 1, 2. 1934 (cytology, as *A. nigricans*).

MATERIAL EXAMINED.—THE NETHERLANDS: on giraffe dung, Zoological Garden, Amsterdam, 1.VII.1959, van Brummelen 693 (L); on lion dung, Zoological Garden, Amsterdam, 16.IV.1970, van Brummelen 2762 (L, also as culture).

GERMAN DEMOCRATIC REPUBLIC: on dung of wild bear (?; Comm. H. Sydow), Tamsel, Brandenburg, 6.XII.1935, Cain (TRTC 34710).

CANADA: on dung of carnivore, W. of Manitowadge, Thunder Bay Dist., Ontario, 18.VI.1963, Cain (TRTC 44832); culture isolated from soil, Winnipeg, III. 1973, J. Reid (CBS 394.73).

U. S. A.: on elk dung, near Elwha River, Olympic National Park, Clallam Co., Washington,

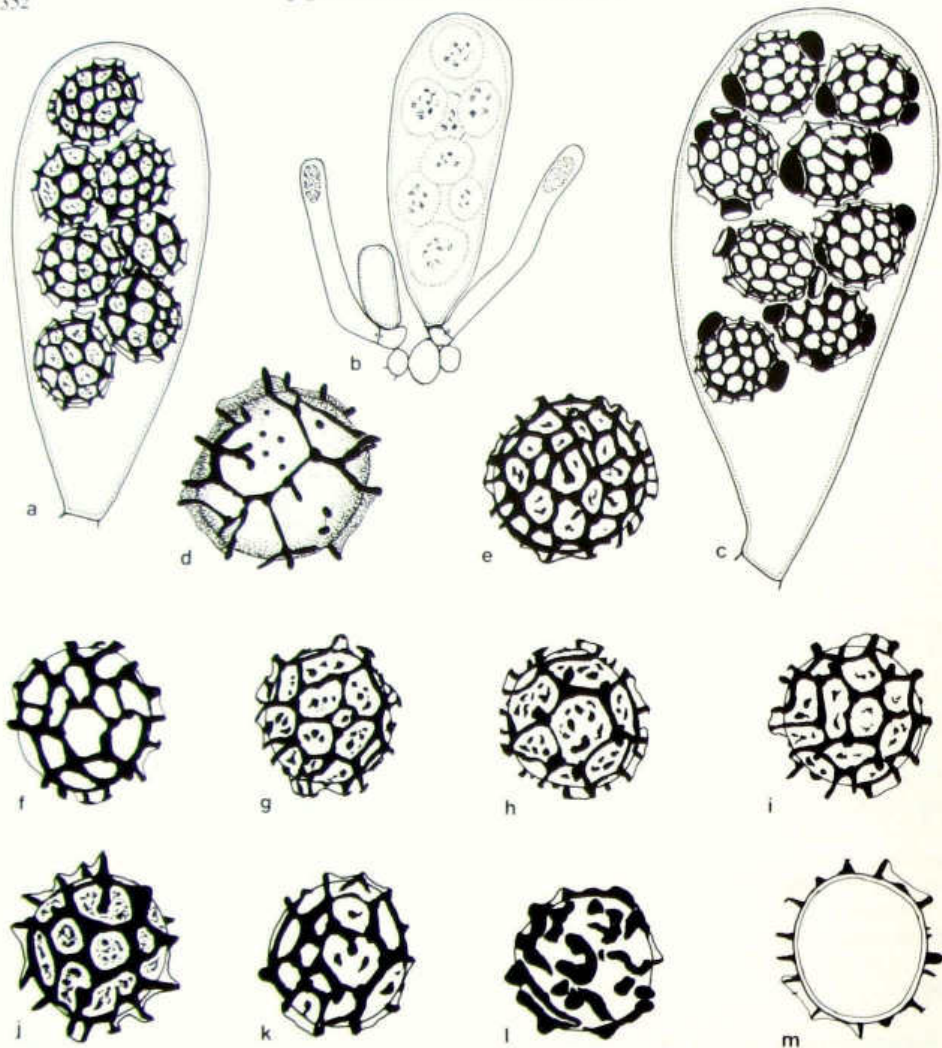


Fig. 6. *Ascodesmis sphaerospora*. —a, c. Asci with mature ascospores  $\times 1000$ . —b. Young ascus and paraphyses  $\times 1000$ . —d-l. Ascospores  $\times 1600$  (in l a rather aberrant type of ornamentation). —m. Ascospore in optical section  $\times 1600$ . (a from van Brummelen 2762, L; b, c from culture 548, Mycothèque PC; d from van Brummelen 693, L; e-m from W. B. Cooke, 27.VI.1955, TRTC 35288.)

21.VIII.1962, Cain C.1849 (TRTC 48381); isolated from trickling filter, Dayton, Montgomery Co., Ohio, 27.VI.1955, W. B. Cooke (TRTC 35288); idem, VI.1955, W. B. Cooke 131E (TRTC 32093; PC-A2250, sent to Madame Le Gal by R. F. Cain; culture 548 in Mycothèque, PC); on dog dung, Cambridge, Massachusetts, II.1887, Thaxter (FH-A3153); on dog dung, Cambridge, Massachusetts, I.1891, Sturgis (NY-A1067, NY-A1068, NY-A1069, TRTC); idem, III.1891 (NY-A1070, TRTC); culture, Cornell Univ., Ithaca, New York, III.1961, R. T. Moore (CBS 125.61, CUP 45103, ATCC 13978, BPI); on Jaguar dung, New York City, VII.1909, Seaver (NY-A1071, TRTC); on tiger dung, VII.1909, Seaver (NY-A1072); on Raccoon-dog dung, Zoo (Bronx, N. Y.), XI.1915, Seaver (NY-A1066, TRTC; type of *Ascodesmis sphaerospora*); culture isolated from rabbit dung, Waco, Texas, 1962, W. G. Fields (CBS 440.74).

BRAZIL: on dog dung, Dois Irmãos, Recife, Pernambuco, 15.XII.1947, Pontual (URM-A284); on jaguar dung (Comm. Dr. A. C. Batista), Recife, s. dat [Obrist] (TRTC 35535); on dung of *Cerdocyon thous* (Comm. A. C. Batista), Recife, III.1960 [Obrist] (TRTC 35593); on dung of American ocelot (*Felis pardalis*) (Comm. A. C. Batista), Recife, s. dat. [Obrist] (TRTC 35598).

When Seaver (1916) published his study on North American species of *Ascodesmis*, he thought that he had recognized *Ascobolus microscopicus* Crouan and placed it in the genus *Ascodesmis* with *Ascodesmis nigricans* as one of the synonyms. Later studies of the type specimen of *Ascobolus microscopicus* by Le Gal (1949) revealed that Seaver had misapplied Crouan's name. Unfortunately, Le Gal did not handle the problem in accordance with the 'International Code of Botanical Nomenclature'.

Obrist (1961: 948) introduced a new name ('nom. nov.') for *Ascodesmis microscopica* (Crouan) Seaver sensu Seaver. In fact, he considered *Ascodesmis microscopica* (Crouan) Seaver to be an unacceptable homonym of '*Ascodesmis microscopica* (Crouan) Le Gal' [= *Ascodesmis microscopica* (Crouan) Seaver sensu Crouan, sensu Le Gal]. In consequence of this, *A. sphaerospora* is typified by the original specimen studied by Seaver. This is one of the two specimens Obrist indicated as type.

*Ascodesmis sphaerospora* has been the object of many investigations on development, cytology, genetics, and ultrastructure, e.g. by Swingle (1934; as *A. nigricans*), Carroll (1967), Brenner & Carroll (1968), O'Donnell & al. (1976), Samuelson (1978), Delattre-Durand & Janex-Favre (1979; as *A. microscopica*).

The present species would appear to be very close to *A. microscopica*, differing only in the subglobular or spherical shape of the ascospores and the more regular net-work of the spore ornamentation.

In this species, the variability in shape and ornamentation of the ascospores is sometimes rather conspicuous. Especially in cultures which have been growing for many generations on artificial media, aberrations may have accumulated. Such a case is found in culture No. 548 of the 'Mycothèque' of the Laboratoire de Cryptogamie in Paris, which was originally isolated, cultured and distributed by W. B. Cooke. The ornamentation of the ascospores is very strongly developed here. Therefore the reticulum may be changed, in the most extreme case, into a single more or less complete layer of vesicles. Such ascospores often show subapical thickenings up to  $5 \mu\text{m}$  high (see Fig. 6c and Delattre-Durand & Janex-Favre, 1979: 59 pl. 4C, E).

*Ascodesmis sphaerospora* is also recorded from Taiwan (Liou & Chen, 1977). It seems to be a cosmopolitan species.

For its delimitation against *A. microscopica*, see under that species.

#### INSUFFICIENTLY KNOWN AND EXCLUDED SPECIES

The following species have been referred to *Ascodesmis* or were, at some time or other, considered to be related to this genus. These species are either excluded because they do not answer to the present concept of *Ascodesmis* or they are doubtful on account of the lack of sufficient descriptions and adequate material.

**aurea.** — *Ascodesmis aurea* Tiegh. in Bull. Soc. bot. Fr. 23: 275. 1876. — Type: not known to be in existence. — Type locality: France.

Van Tieghem (l.c.) gives only a short and very fragmentary description of this species. He merely compares some characters of it with *A. nigricans*, which is more fully described. The fruit bodies are very small, golden yellow and the ascospores are spherical, only 6 µm across with an ornamentation of more strongly coloured golden yellow dots.

According to Dangeard (1910: 247) *A. aurea* is only a young *A. nigricans* in which the fruit bodies have not yet attained their definitive brown colour. This supposition, however, is very unlikely since young ascospores in *Ascodesmis* are not considerably smaller than mature ones while the pigment of the spore ornamentation is brown and manifests only very shortly before maturity.

The original description could even include some members of the Gymnoascaceae.

Because of the very insufficient description and the lack of material *A. aurea* should be regarded as a nomen dubium.

**brachyascus.** — *Lasiobolus brachyascus* March. in Bull. Soc. R. bot. Belg. 24: 73. 1884. — *Cubonia brachyasca* (March.) Sacc., Syll. Fung. 8: 527. 1889. — Type: not known to be in existence. — Type locality: Werbomont (Liège), Belgium.

The type specimen of this species is neither preserved in the Marchall herbarium at Meise (BR), Gembloux nor in the Saccardo herbarium at Padua (PAD).

*Lasiobolus brachyascus* was selected as type of the genus *Cubonia* Sacc. by Clements & Shear (1931). Other species of *Cubonia*, like *Cubonia dentata* Boud. and *C. hyracis* Faurel (cf. Durand, 1973), with a strongly developed receptaculum, an excipulum and flesh, and cleistohymenial ascomata opening in the mid-meso-hymenial phase, do certainly not belong to the same genus, and should probably be placed among the 'Ascophani' with spherical ascospores.

*Cubonia boudieri* (Renny apud Phill.) Sacc. proved to be a synonym of *Ascobolus brassicae* Crouan (van Brummelen, 1967: 91).

Seaver (1928) inserted *Cubonia* in his 'North American Cup-fungi' but had not seen any typical material.

Bezerra & Kimbrough (1975) in their monograph of the genus *Lasiobolus* Sacc. did not accept *C. brachyasca* in this genus.

The following characters might suggest an eventual relationship of *C. brachyasca* with *Ascodesmis* (van Brummelen, 1967): (1) the small fruit bodies (120–200 µm diam.), (2) the obovoid-pyriform, protruding asci (40–45 × 19.5–21.5 µm) not staining blue with iodine, (3) the spherical ascospores (8.8–9.2 µm diam.), roughened with small dots, and (4) the growth on dog dung. However, the presence of an excipulum clothed with long hyaline hairs, strongly curved paraphyses and hyaline ascospores are contrary to such a relationship.

Until material of this species is found again, *Cubonia brachyasca* and *Cubonia* will remain doubtful names.

**canina.** — *Ascodesmis canina* Jeng & Cain in Mycotaxon 3: 392, fs. 1–14. 1976. — Holotype: Dumont & al. VE-4338b (TRTC).

This fungus shows a relatively well-developed receptaculum with an excipulum of textura prismatica or porrecta (cf. Jeng & Cain, l.c.: f. 2). Young ascospores are hyaline and surrounded by a gelatinous layer.

The pigment is present in an almost continuous, rather uniform, 0.7–1.3 µm thick layer of

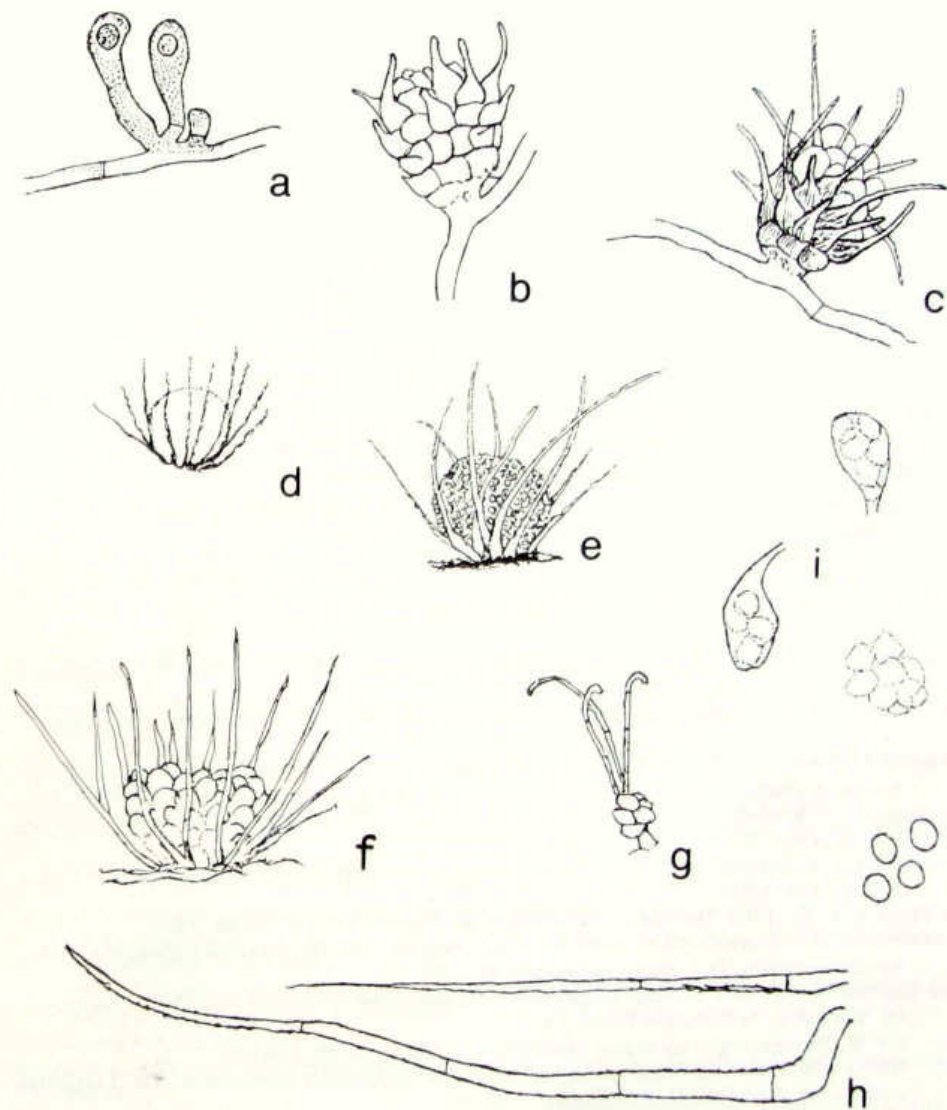


Fig. 7. *Ascodesmis volutelloides*. — a. Initials. — b–c. Young fruit bodies. — d–f. Fruit bodies. — g. Paraphyses. — h. Hairs. — i. Ascus and ascospores. (Redrawn after original drawings in Masee herbarium, NY.)

brown granules. Only incidental holes, pores, and small fissures occur in this layer, giving the secondary wall of mature ascospores a more or less perforated aspect.

This type of ornamentation and pigmentation are characteristic of *Ascobolus* Hooker per Pers. The paragymnohymenial ascomata, the texture of the excipulum and the shape of the asci show its relationship with *Ascobolus* sect. *Pseudascodesmis* Brumm.

The new name *Ascobolus perforatus* Brumm., *nom. nov.*<sup>1</sup> is proposed for this species.

**volutelloides.** — *Ascodesmis volutelloides* Mass. & Salmon in *Annls Bot.* **16**: 61, pl. 4 fs. 13–17. 1902. — Type: not known to be in existence. — Type locality: Kew, England.

Besides the published illustrations of this species, a series of drawings are preserved in the Massee herbarium (NY). These drawings give a more complete picture of the development of the fruit bodies but are insufficient in the details of asci and ascospores (Fig. 7).

In certain characters, this fungus resembles *Ascodesmis*, e.g. in: the small fruit bodies (c. 150 µm diam.), (2) the pyriform to oblong asci (28–35 × 14–16 µm), and (3) the spherical ascospores (10 µm diam.). Other characters, however, like the presence of (1) long seta-like, septate hairs on the outside, (2) hyaline or pale straw-coloured ascospores, (3) curved, evanescent paraphyses, and (4) the development of fruit bodies only after some months, are contrary to a position in that genus.

The asci are probably not operculate. A certain similarity is observed with *Cubonia brachyasca* (see above) and both might very well be congeneric.

A position of *A. volutelloides* in the Gymnoascaceae, as proposed by Massee & Salmon (l.c.), is not unlikely.

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<sup>1</sup> Basionym: *Ascodesmis caninus* Jeng & Cain in *Mycotaxon* **3**: 392. 1976; not *Ascobolus caninus* Fuckel in *Hedwigia* **5**: 3. 1866 not *Ascobolus caninus* Auersw. in *Hedwigia* **7**: 52. 1868.

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