

THE GENUS ASCODESMIS¹

WALTER OBRIST²

Abstract

A study of the physiological, cytological, and morphological characteristics of four species of the genus *Ascodesmis* has been made. The genus represents a highly specialized coprophilous group of the operculate discomycetes, probably belonging to the Humariaceae. A new specific name (*Ascodesmis sphaerospora* nom. nov.) and a new species (*Ascodesmis macrospora* sp. nov.) are proposed.

Introduction

Ascodesmis van Tieghem is a genus of the operculate discomycetes characterized by the lack of an excipulum. It was, therefore, considered to represent a primitive form of the ascomycetes. Cytological investigations carried out by Claussen (1905) and Swingle (1934) appeared to prove this hypothesis. But Le Gal (1949) claims, on account of the complicated spore structure, that the genus is more likely to be a higher but regressive form. This author also clarified the taxonomic position of two species, which had been misinterpreted.

While investigating coprophilous ascomycetes on dung of brazilian animals, I succeeded in isolating several strains of *Ascodesmis* species. A study of these isolates has been made in an attempt to further clarify the phylogenetic position and species concept of the genus.

Spore Germination

Discharged ascospores of any species of *Ascodesmis* will readily start germinating within a few hours in a moist environment. Immersed in any liquid, however, the spores do not germinate. Dried spores can be revived even after a period of many years. Three-year-old spores of *Ascodesmis sphaerospora* did germinate in our experiment.

Before forming the germ tube, the spore swells considerably and the spore wall turns brighter. The average diameter of spores of *A. sphaerospora* that had just started to form a germ tube (i.e. 6–12 hours after discharge) was 14–15 μ , compared to 10–11.5 μ at the time of discharge. Each spore produces one, rarely two, germ tubes, which grow fast and soon become septate.

The branching and further growth of the hyphae is well described by Claussen (1905).

Cultural Studies

All described species of *Ascodesmis* are coprophilous and have been found on dung of herbivorous and carnivorous animals. In cultural studies dung decoction agar has been used exclusively by previous workers (Claussen 1905, Swingle 1934). An attempt has therefore been made to grow the species in

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Contribution from the Department of Botany, University of Toronto, Toronto 5, Ontario.

²National Research Council of Canada. Postdoctorate Fellow, 1959–61. Present address: Eidg. Anstalt für Wasserversorgung, Abwasserreinigung und Gewässerschutz (EAWAG), Swiss Federal Institute of Technology, Zürich, Switzerland.

better-defined media. The four species *A. nigricans*, *A. sphaerospora*, *A. macrospora*, and *A. porcina* all grow well on various artificial media and do not show any difference from each other regarding both vegetative growth and production of ascocarps in any one medium. Of the numerous media tested, however, two groups can readily be distinguished regarding the abundance of growth and fruiting of *Ascodesmis* species:

1. Plain agar, malt agar, peptone agar, peptone - malt agar, V-8 agar. Fast mycelial growth in and on surface of medium, poor fruit body production.

2. Modified Leonian's (peptone, maltose, malt extract, yeast extract), soluble starch - yeast extract - agar. Fast growth and abundant aerial mycelium, fruiting very plentifully.

The last-mentioned medium proved most satisfactory and its formula is therefore given here: soluble starch, 10.0 g; yeast extract, 5.0 g; KH_2PO_4 , 1.0 g; $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 0.5 g; agar, 20.0 g; tap water, 1000 ml.

In mixed cultures in which *Ascodesmis* is grown with bacteria isolated from dung, production of apothecia is increased, whereas mycelial growth is not affected. The above-mentioned soluble starch - yeast extract medium was used, and unidentified dung bacteria were grown in petri dishes in small colonies about three days before inoculation of an *Ascodesmis* species. The fungus mycelium spread rapidly from a central point. Abundant but scattered production of fruit bodies started after 1-2 days and mature ascospores appeared after 3-6 days. On the bacterial colonies, however, apothecia appeared densely clustered and mature spores were produced about one day earlier.

Similar experiments were made with liquid media in tubes and strips of filter paper soaked in liquids.

Three kinds of liquid media were used:

A. Minerals, peptone, malt extract, distilled water.

B. A + yeast extract.

C. Dung bacteria grown for 3 days in liquid B were autoclaved.

Inoculations of *A. porcina* grew slowly in the liquids but rapidly on the filter paper strips above the liquids. The results are shown in Table I.

TABLE I
Ascospore production in *A. porcina* in liquid media

	Days required for production of mature spores		
	A	B	C
Liquid medium	—	20-24	12-15
Liquid medium + filter paper strips	25-38	5-7	4-5

It seems from these experiments that chemical factors stimulating apothecial development are supplied by bacteria in the natural habitat and that yeast extract is the most suitable, although not as efficient, substitute. Solid media are superior to liquids.

In all four species studied the production of fruit bodies in pure cultures slowly decreases after many transfers. There is an increase in the growth of aerial mycelium and most apothecia are formed immersed in the medium.

The culture of *A. nigricans* isolated by Le Gal (1949) has almost ceased to produce fruit bodies on agar media. It can be revived, however, if it is grown on sterilized dung together with bacteria.

Strains of the four *Ascodesmis* species studied are therefore better maintained in mixed cultures with bacteria isolated from dung. Production of ascocarps in such cultures remained abundant after many transfers.

Light is not required for either formation or maturation of ascospores. Monospore cultures grown without light in a thermostat at 20° C produced mature spores with normal germinating capacity. The time between inoculation and discharge of mature ascospores, however, is 1–3 days longer than in a control culture under daylight.

Similar experiments were made in a group of coprophilous pyrenomycetes, the Sordariaceae, by Moreau (1953). Whereas the Sordariaceae have almost identical nutrient requirements and are also stimulated by other microorganisms, they differ from *Ascodesmis* in that they require light for fruiting.

Cytology and Genetics

Because of the lack of an excipulum, *Ascodesmis* species seem to be very suitable for cytological work. Van Tieghem (1876) and Zukal (1886) did not observe any sexual stages. Dangeard (1903, 1907) first saw pairs of coiled hyphae growing out of short side branches but claimed that there was no fusion between these structures, the only sexual fusion of nuclei taking place in the young asci. Claussen (1905) and Swingle (1934), however, observed nuclear fusions both between the coiled hyphal pairs (ascogonium and antheridium) and in the young asci. Since it is very difficult to demonstrate such fusions with convincing evidence because (1) all cells are multinucleate and (2) the coiled hyphal pairs occur in dense clusters in which cell walls seem to disintegrate, this problem remains unsolved.

A genetical study would probably be a better approach to these problems. An attempt was made to obtain mutant strains. Monospore cultures of *A. sphaerospora* and *A. macrospora* were subjected to irradiation with ultraviolet light. Exposures of 3–10 hours failed to induce any morphological mutation.

Hyphal fusions are quite frequent in all species studied. Such fusions seem to stimulate ascocarp production. In order to investigate the occurrence of interspecific anastomosis, all possible combinations of strains of two different species were mated in petri-dish cultures. In each case the mycelia grew together without any sign of inhibition. The analysis of fruit-bodies along the borderline always showed that the spores of all asci in any one apothecium belonged to either one or other of the two species mated. No intermediate or unidentified spores were observed. The species as described in this paper, therefore, seem to be genetically distinct and non-hybridizing. This problem, however, deserves a more extensive study.

Asci and Spores

Shape, size, and structure of the asci are almost uniform in the genus *Ascodesmis*. The shape is very broadly clavate, the apical structure is typically of the operculate type of the discomycetes, and before discharging the spores, the asci swell considerably and project from the hymenium.

The spores are crowded in a gelatinous mass and are all discharged together in a group. In a culture of *A. macrospora*, a maximum vertical discharge distance of 20 cm has been measured. The asci bow towards the light. Under cultural conditions, the asci shoot their spores when the cover is removed. A slight air current brings about the rupture of the operculum of swollen asci. In many asci, however, the turgor pressure breaks down before the operculum is opened and the spores remain in the ascus. In each species, the asci mature successively. In this manner, spores are released from one apothecium over a period of many hours to a few days if conditions are favorable.

The spore number is usually eight, but numbers of four and five have been observed especially in cultures on dung and on media of group 1. Anomalous small and dark spores occur in numbers of one to three per ascus in *A. sphaerospora* and *A. macrospora* (Fig. 3). In rich media (group 2) these anomalies are less frequent. Monospore cultures of anomalous spores have not been made, but they are likely not to be capable of germination.

The spore features seem to be the only differentiating characters between the species. Shape, size, and markings of the spores are quite typical in each specimen or culture, but if many collections are examined, one is confused because of the considerable variability. Shape and size can be accurately measured (Fig. 1); the different types of spore markings, however, are difficult to separate. There is a general tendency towards reticulate markings, *A. nigricans* showing the least amount of reticulation and *A. sphaerospora* the most perfect pattern.

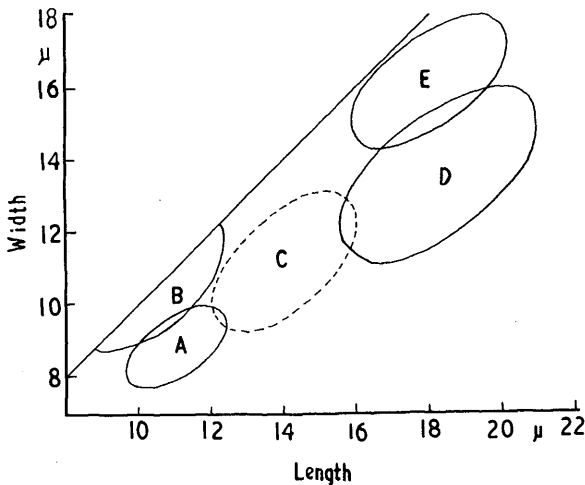


FIG. 1. Spore measurements in artificial culture.
 (A) *Ascodesmis nigricans* and *Ascodesmis porcina*,
 (B) *Ascodesmis sphaerospora*,
 (C) *Ascodesmis microscopica* (measurements from Le Gal 1949),
 (D) *Ascodesmis macrospora*,
 (E) strain TRTC 35537, *Ascodesmis macrospora*, in natural habitat.

Le Gal (1949) recommends the use of cotton blue for staining the spore markings. This stain is useful for the light brown spores of *A. nigricans* and

for immature spores. The perisporium, a hyaline sheath surrounding the spores of *A. microscopica* and *A. macrospora*, will stain slightly greyish. The dark brown reticulations of fully mature spores of *A. sphaerospora* and *A. macrospora*, however, are not stained by cotton blue.

Description of the Genus *Ascodesmis*

Mycelium hyaline, septate, multinucleate, branching monopodially, growing circularly on agar media, spreading rapidly. No conidia or spermatia produced. Ascocarp initials consisting of one to three (mostly two) short hyphal side branches, branching dichotomously and producing more slender branches which coil around each other in pairs.

Apothecia minute, globose, scattered or gregarious, hyaline, without excipulum, consisting of a cluster of asci and surrounding paraphyses springing from a clump of basal cells.

Asci broadly clavate, ovoid or elliptical, fasciculate, maturing successively, rounded above, opening by a somewhat obliquely attached operculum, thin-walled, contracted below into a short stipe, swelling before spore discharge, not stained by iodine, eight- (exceptionally four- to five-) spored. Paraphyses numerous, stout, enlarged above, septate, unbranched, originating from the lower cells of the basal cell mass.

Spores one-celled, spherical to ellipsoid, hyaline when young, becoming brown at maturity, two-seriate or irregularly arranged, crowded together in upper part of ascus before discharge, shot off together, covered with dark brown markings in the form of spines, ridges, or reticulations, with or without hyaline perisporium.

Type species: *Ascodesmis nigricans* van Tieghem.

KEY TO THE SPECIES

1. Spores partially or entirely surrounded by a hyaline outer membrane, the perisporium; longer than 12.5μ 2
1. Spores without perisporium; length up to 12.5μ 3
2. Spores $12.5-16 \mu$ long, completely covered by perisporium..... *A. microscopica*
2. Spores $16-21 \mu$ long, partially covered by perisporium..... *A. macrospora*
3. Spores globose or subglobose (difference between length and width less than 1.5μ), with reticulate markings..... *A. sphaerospora*
3. Spores ellipsoid, never reticulate..... 4
4. Spore markings consisting of spines and short angled ridges..... *A. nigricans*
4. Spore markings consisting of spines and one longitudinal ridge..... *A. porcina*

Ascodesmis nigricans van Tieghem (Fig. 10)

SYNONYMS: ? *Ascodesmis echinulata* Bainier. Bull. Soc. Myc. Fr. 23:137, 1907.

Ascodesmis nigricans van Tieghem. Bull. Soc. Bot. Fr. 23:275, 1876.

HABITAT: Dung of dog, sheep, goat, pig, fox, peccary, jaguar, ocelot.

NEOTYPE: Culture No. 100, Laboratoire de Cryptogamie du Museum Nationale d'Histoire Naturelle, Paris, Le Gal (1949).

SPECIMENS EXAMINED: Neotype. On fox dung, Nashville, York Co., Ontario, May 20, 1956, R. F. Cain (TRTC 32679). On dog dung, Nashville, York Co., Ontario, Dec. 5, 1959, R. F. Cain (TRTC 35292). On dung of jaguar (TRTC 35536), Ocelot (TRTC 35599), and peccary (TRTC 34759), Recife, Brazil, June 27, 1957, A. C. Batista. On dung of carnivorous animal, Colfax, La., U.S.A., Aug. 26, 1960, R. F. Cain (TRTC 36466).

Apothecia $80-180 \mu$. Asci $42-57 \times 18-25 \mu$. Paraphyses $3-5 \mu$, slightly enlarged above (up to 5.5μ).

Spores ellipsoid, without markings $9.5\text{--}11.5 \times 8\text{--}10 \mu$, with markings $11.5\text{--}12.5 \times 9\text{--}10.5 \mu$, difference between length and width more than 1.5μ , pale brown at maturity. Sculpturing consisting of spines, wart-like projections, short ridges, or irregularly angled ridges (see Le Gal 1949 and Fig. 10).

According to Le Gal (1949) van Tieghem's type specimen is lacking. It is suggested, therefore, that Le Gal's specimen be designated the neotype of the species.

Ascodesmis sphaerospora nom. nov. (Figs. 2-9)

SYNONYM: *Ascodesmis microscopica* (Crouan) Seaver. Mycologia, 8:3, 1916.
non *Ascodesmis microscopica* (Crouan) Le Gal. Rev. Myc. 14:93, 1949.

HABITAT: Dung of various animals (dog, wild boar, jaguar).

TYPE: Culture isolated from sewage trickling filter; Dayton, Montgomery Co., Ohio, June 1955, Wm. B. Cooke (TRTC 32092).

SPECIMENS EXAMINED: Type. On dog dung, Cambridge, Mass., 1891, W. C. Sturgis (Herb. N.Y. Botanical Garden). On dung of raccoon-dog, Bronx Zoological Garden, N.Y., Nov. 1915, F. J. Seaver, type of *Ascodesmis microscopica* (Crouan) Seaver (Herb. N.Y. Botanical Garden). On dung of wild boar, Tamsel, Brandenburg, Germany, Febr. 22, 1935, P. Vogel, developed in laboratory, Toronto, Ont., Dec. 6, 1935, R. F. Cain (TRTC 34710). On dung of jaguar (TRTC 35535) and ocelot (TRTC 35598), Recife, Brazil, June 27, 1957, A. C. Batista. On dog dung, Nashville, York Co., Ont., Dec. 5, 1959, R. F. Cain (TRTC 35293). On dung of carnivorous animal, Colfax, La., U.S.A., Aug. 26, 1960, R. F. Cain (TRTC 36467).

Mycelia hyalina, tenua, sine conidiis et spermatis. Ascogonia in ramis lateralibus disposita. Apothecia minuta, subglobosa vel hemisphaerica, gregaria, $80\text{--}150 \mu$ diam., superficialia, hyalina, ex fasciculis (3)– $10\text{--}18$ ascorum et numerosorum paraphysium circumdatorum ex gleba basali crescentibus composita. Asci clavati vel elliptici, $55\text{--}80 \times 24\text{--}33 \mu$, fasciculati, apice rotundati, in stipitem brevem contracti, operculati, unitunicati, tunica tenui (solum in parte basali densata) praediti, octospori, raro 4–5-spori, in ordinem maturescents. Paraphyses numerosi, hyalini, septati, $3.5\text{--}5 \mu$ diam.; in apice ad 6μ densati, circa ascos dispositi.

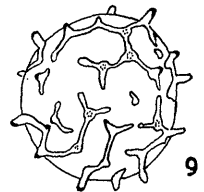
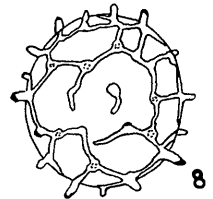
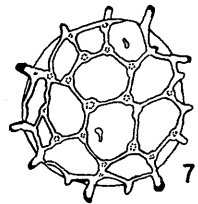
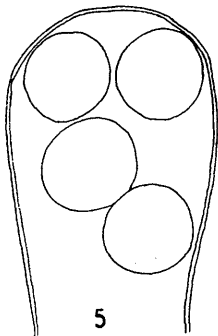
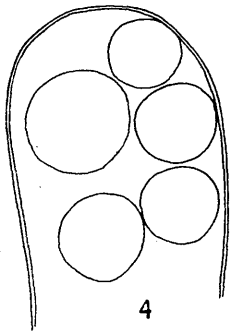
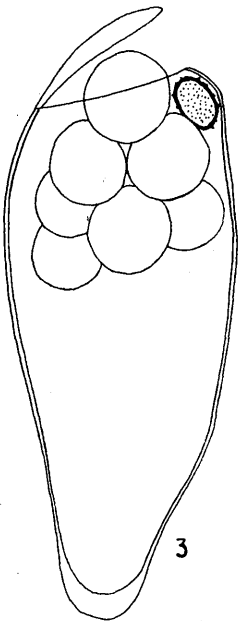
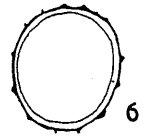
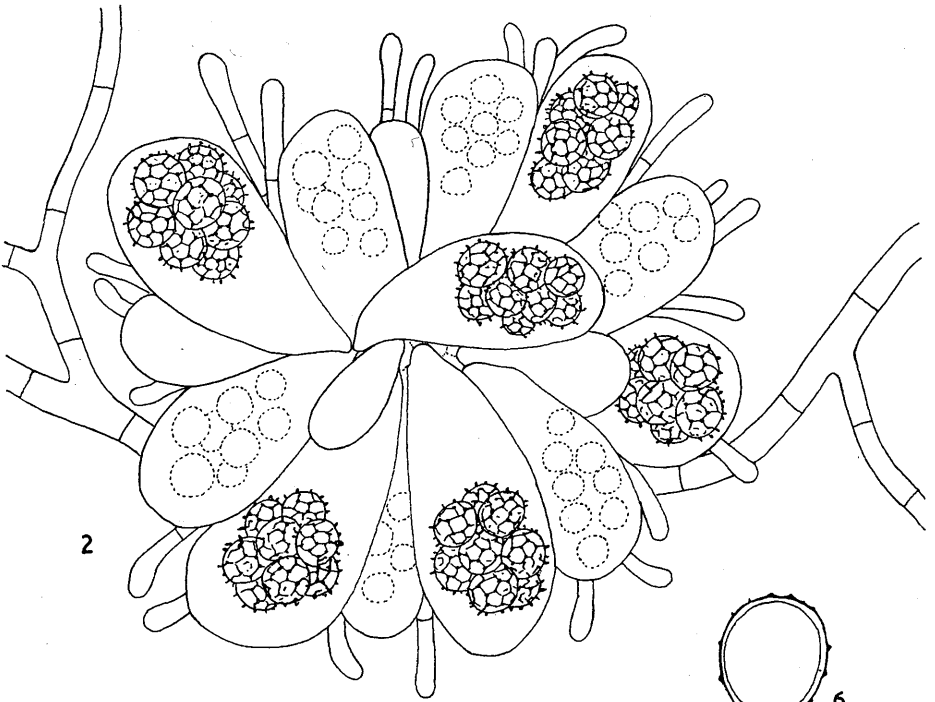
Ascosporae unicellulares, globosae vel ellipticae, cum spinis $11\text{--}15 \times 10.5\text{--}14 \mu$, sine spinis $8.5\text{--}12.5 \times 8.5\text{--}12 \mu$, cohaerentes, primum hyalinae, maturitate atrofuscae, areolatae, aculeatae, reticulatae, episporio tenui.

Apothecia minute, hemisphaerical to subglobose, $80\text{--}200 \mu$ in diameter, scattered or gregarious, hyaline, superficial, without excipulum, with many asci surrounded by paraphyses.

Asci broadly clavate, oblong or ovoid, $55\text{--}80 \times 24\text{--}33 \mu$, fasciculate, rounded above, opening by a slightly obliquely attached operculum, thin-walled, contracted below into a short, thick-walled stipe, eight-, exceptionally four- or five-spored, maturing successively, $10\text{--}18$ (sometimes less) visible at one time, three-eight with mature spores. Before spore discharge, the asci swell to a length of up to 92μ , the operculum is then opened and the spores shot off altogether through internal pressure.

Paraphyses numerous, stout, $3.5\text{--}5 \mu$ in diameter, gradually enlarged above (up to 6μ), in culture sometimes forming globose endings of $6\text{--}8 \mu$, septate, unbranched, slightly longer than the asci.

FIGS. 2-9. *Ascodesmis sphaerospora*. Fig. 2. Apothecium seen from above ($\times 500$). Fig. 3. Ascus with one anomalous small spore ($\times 1000$). Figs. 4 and 5. Asci with fewer than eight ascospores ($\times 1000$). Fig. 6. Young ascospore in optical section ($\times 2000$). Figs. 7-9. Mature ascospores ($\times 2000$).



Spores one-celled, spherical to ellipsoid, with markings $11-15 \times 10.5-14 \mu$, without $8.5-12.5 \times 8.5-12 \mu$, if elliptical, difference between length and width always less than 1.5μ , biseriate or crowded together, first hyaline, then pale brown, becoming dark brown at maturity. Sculpturing consisting of net-like, dark brown reticulations (meshes reaching a diameter of $2-3.5 \mu$) and (or) irregular ridges, the reticulations and ridges projecting about the periphery of the spore and forming spines (length up to 2μ) at their junctions. Spore wall thick in young spores, thin in mature spores. No perisporium. Cotton blue stains only immature spores.

This fungus has apparently been misinterpreted by Seaver (1916). The reinvestigation of *Ascodesmis microscopica* (Crouan) by Le Gal (1949) has shown that Seaver's species can be neither *A. nigricans* nor *A. microscopica*. Unfortunately, in many mycological textbooks Seaver's combination *A. microscopica* has been used (e.g. Alexoupoulos 1952, Gray 1959, Wolf and Wolf 1947). *A. nigricans* differs in having non-reticulate spores, *A. microscopica* (Crouan) Le Gal in producing a perisporium. In addition, the spores of these two species are typically ellipsoid.

Ascodesmis sphaerospora shows a considerable variation in number, size, and shape of the ascospores. If growing on dung the spores are spherical or nearly so, whereas on artificial agar media they tend to be more elliptical. Four-spored asci are rather rare, the five-spored asci occurring more frequently, but both of these anomalies have not been observed in agar cultures. Single, imperfectly developed spores in eight-spored asci, however, can be found on any medium quite often, these spores being small ($5-7.5 \mu$), very dark and with reduced, indistinct sculpturing (see Fig. 3). The spore sculpturing may vary from regular reticulations to irregular, angled ridges. The relatively long spines are a constant feature in this species.

Ascodesmis porcina Seaver (Fig. 11)

HABITAT: Dung of pig, peccary, horse.

TYPE: On pig dung from Puerto Rico, grown in the laboratories of the New York Botanical Garden, Jan. 1915, F. J. Seaver (Herb. N.Y., Botanical Garden).

SPECIMENS EXAMINED: Type. On pig dung from New Jersey, Nov. 26, 1915, F. J. Seaver (Herb. N.Y. Botanical Garden). On dung of peccary, Recife, Brazil, June 27, 1957, A. C. Batista, developed in laboratory, Toronto, Aug. 17, 1960 (TRTC 36308).

Apothecia $80-200 \mu$. Asci $55-65 \times 22-28 \mu$, 7-18 visible at one time, two to seven of them with mature spores, swelling before spore discharge to a length of up to 75μ . Paraphyses not numerous, stout, $3.5-5 \mu$ in diameter, slightly enlarged above (up to 5.5μ).

Spores with markings $12.5-15 \times 10-11 \mu$, without $10-12.5 \times 8-9 \mu$, pale brown at maturity. Sculpturing consisting of rounded, wart-like projections and short interrupted ridges, usually with one conspicuous simple or branched ridge extending longitudinally across one side of the spore (see Fig. 11).

Since Seaver's (1916) original description, this species has been reported only by Meyer and Meyer (1949) on horse dung from Panama and by Gunnell (1960) from Great Britain. It is, therefore, likely to be widely distributed throughout the world. The spore markings are of a very peculiar type and readily separate the species from any other. Size, shape, and color of the spores agree very closely with *A. nigricans*.

Ascodesmis microscopica (Crouan) Le Gal

SYNONYMS: *Ascobolus microscopicus* Crouan. Ann. Sc. Nat. 4. sér. Bd. 7:175, 1857.

Boudiera microscopica (Crouan) Cooke. Grevillea, 6:76, 1877.

Ascodesmis microscopica (Crouan) Le Gal. Rev. Mycol. 14:93, 1949.

Boudiera Claussenii Hennings. Beibl. Hedwigia, 42:182, 1903.

HABITAT: Dung of various kinds.

TYPE: *Ascobolus microscopicus* Crouan, "sur l'Album graecum, près Brest", in herbarium Montagne, Museum Nationale d'Histoire Naturelle, Paris.

Apothecia 200–300 μ . Asci broadly clavate, 63–80 \times 26–33 μ . Spores subglobose to ellipsoid, without markings 12.5–16 \times 9.5–13.25 μ , with markings 14–18.5 \times 11–15 μ , at maturity dark brown, sculpturing consisting of irregular reticulations, short ridges and spines, surrounded by a perisporium, which is stained by cotton blue.

The type of this species has been reinvestigated and described by Le Gal (1949).

Ascodesmis macrospora sp. nov. (Fig. 12)

HABITAT: Dung of mountain lion and jaguar.

TYPE: TRTC 35512. Culture isolated from dung of mountain lion (*Felis concolor*), Recife, Brazil, June 27, 1957, A. C. Batista, developed in moist chamber, Toronto, Jan. 25, 1960.

OTHER SPECIMENS EXAMINED: On dung of jaguar (TRTC 35537) and Raposa do campo (*Cerdocyon thous*) (TRTC 35596), Recife, Brazil, June 27, 1957, A. C. Batista, developed in laboratory, Toronto, 1960.

Mycelia hyalina, tenua, sine conidiis et spermatiis. Ascogonia in ramis lateralibus disposita.

Apothecia minuta, subglobosa vel hemisphaerica, gregaria, 90–200 μ , diam., superficialia, primum hyalina, maturitate atrofusca, ex fasciculis (5) 10–20 ascorum et numerosorum paraphysorum exgleba basali crescentibus composita. Asci clavati vel elliptici, 72–90 \times 25–35 μ , fasciculati, apice rotundati, in stipitem brevem contracti, operculati, unitunicati, tunica tenui (in parte basali densata) praediti, octospori (raro 4–5-spori), in ordinem maturescentes. Paraphyses numerosi, hyalini, septati, 4–5.5 μ diam., circa ascos dispositi.

Ascosporae unicellulares, ellipticae, cum spinis 18.5–23 \times 14–16.5 μ , sine spinis 16–21 \times 12–15.5 μ , cohaerentes, irregulariter dispositae, primum hyalinae, maturitate atrofuscae, reticulatae, aculeatae, episporio tenui et in parte perisporio hyalini circumventae.

Mycelium in culture hyaline, branching monopodially, spreading rapidly. No conidia or spermata produced. Ascogonia and antheridia as side branches growing side by side on mycelium, forming dichotomously branching structures, the ends of which coil around each other in pairs.

Apothecia minute, hemispherical to subglobose, 90–200 μ , in diameter, scattered, first hyaline, becoming dark brown at maturity, superficial (in culture also immersed), without excipulum, the asci surrounded by paraphyses. Asci broadly clavate, oblong, elliptical or ovoid, 72–90 \times 25–35 μ , fasciculate, rounded above, opening by a slightly obliquely attached operculum, thin-walled, contracted below into a short, thick-walled stipe, eight- (exceptionally four- to five-) spored, maturing successively, 10–20 visible at one time, three to nine of them with mature spores, swelling before spore discharge to a length of up to 110 μ .

Paraphyses numerous, stout, $4-5.5 \mu$ in diameter, very slightly enlarged above (up to 6μ), septate, unbranched, growing up earlier than the asci.

Spores one-celled, elliptical, with markings $18.5-23 \times 14-16.5 \mu$, without markings $16-21 \times 12-15.5 \mu$, crowded together, first hyaline, then pale brown, becoming dark brown at maturity. Sculpturing consisting of irregular or interrupted, net-like reticulations (meshes with a diameter of $3-7 \mu$), short ridges, and scattered spines. Parts of the spore surface covered by a hyaline, gelatinous perispodium. Spores discharged at once through opening of operculum (Fig. 12).

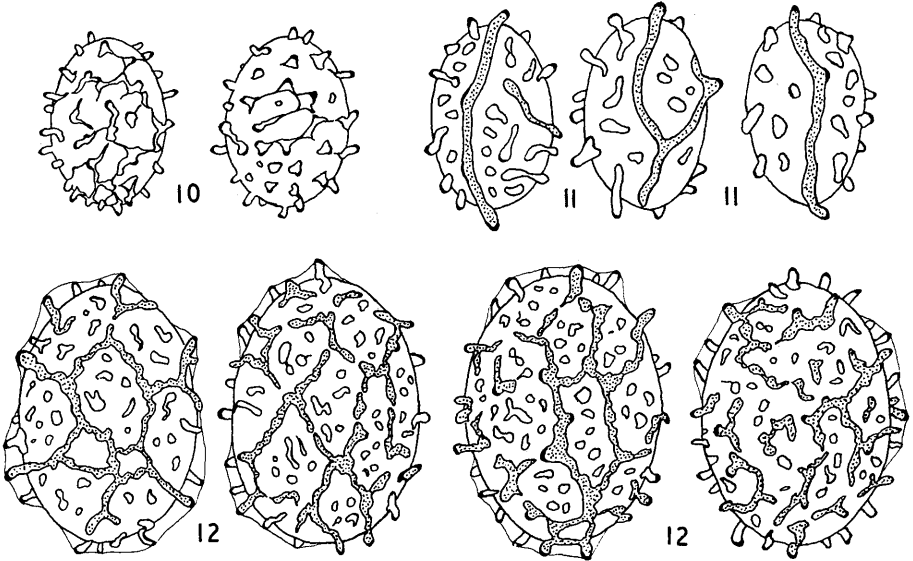


FIG. 10. Ascospores of *Ascodesmis nigricans* ($\times 2000$).

FIG. 11. Ascospores of *Ascodesmis porcina* ($\times 2000$).

FIG. 12. Ascospores of *Ascodesmis macrospora* ($\times 2000$).

This species resembles *A. microscopica*, but the spores are larger and only partially covered by a hyaline perispodium.

Conclusions

1. The species studied show almost identical physiological and cytological properties. The genus is highly specialized in its coprophilous habitat. Certain growth factors required are probably supplied by other microorganisms, particularly bacteria.

2. *A. nigricans*, *A. sphaerospora*, and *A. macrospora* are homothallic. All species studied have multinucleate cells and the ascocarps develop in the same manner as described by earlier workers.

3. Morphological characters useful for separation of species are size, shape, structure, and markings of the spores.

4. *Ascodesmis* species investigated under the name *A. nigricans* by Dangeard (1903, 1907) and Claussen (1905, 1912) is probably *A. microscopica*, while that investigated by Zukal (1886) and Swingle (1934) is probably *A. sphaerospora*.

5. On account of the physiological specialization and the complicated spore structure it is believed that the genus *Ascodesmis* represents a high evolutionary level rather than a primitive form of the operculate discomycetes (a hypothesis established by Le Gal, 1949).

6. The relationship of the genus can not be determined with our present knowledge. The spore structure suggests a relationship to *Boudiera* and *Lamprospora*. Therefore, the genus *Ascodesmis* may be tentatively placed in the family Humariaceae, tribe Humarieae sensu Le Gal (1947). The family Pyronemaceae sensu Grelet (1945) and the tribe Pseudo-Ascoboleae sensu Le Gal (1947) are probably artificial groupings.

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