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R. K. Benjamin

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A NEW GENUS OF THE GYMNOASCACEAE WITH A REVIEW OF THE OTHER GENERA

R. K. BENJAMIN

Whenever fungi referable to the Gymnoascaceae have been encountered by the writer an attempt always has been made to isolate and grow them in pure culture, and species representing most of the recognized genera usually included in the family have been collected. In addition, the author has received numerous isolates from other students of the fungi, and in this regard he is indebted especially to Drs. K. B. Raper, C. W. Emmons, and C. W. Hesseltine.

When Baranetzky founded the Gymnoascaceae (1872) he included therein not only his newly described Gymnoascus but also such genera as Endomyces, Saccharomyces, and Taphrina. Eidam (1880) excluded Endomyces and Saccharomyces from the family, retained Gymnoascus and Taphrina, and added Ascodesmis, described four years earlier by Van Tieghem (1876), and a new genus Ctenomyces. Schroeter's treatment of the Gymnoascaceae published in 1893 established a concept of the family which has remained essentially unchanged to the present, i.e. it includes those simple cleistocarpous ascomycetes in which the fructification consists of a loosely interwoven mass of more or less modified hyphae forming an imperfect peridium about the ascigerous tissue. In Schroeter's work five genera were considered: Ctenomyces Eidam, Gymnoascus Baran., Myxotrichum Kze., Amauroascus Schroet., and Arachniotus Schroet.; the latter two genera were established as new and based for the most part on entities described earlier by Eidam (1886) and Van Tieghem (1877) as species of Gymnoascus.

Kunze was the first to describe species of fungi which now are included in the Gymnoascaceae when he characterized Myxotrichum chartarum and M. murorum in 1823. Fries (1832) included these and eight more species of his own description in his treatment of the genus. The true relationship of many of Fries' species is uncertain. Myxotrichum aeruginosum Montagne (1836) and M. deflexum Berkeley (1838; later described as *Eidamella spinosa* by Matruchot and Dassonville, 1901) were added next, and in 1860 Berkeley described Arthroderma curreyi which subsequently was redescribed by Eidam (1880) as the sexual phase of his Ctenomyces serratus (see below). Following the description of Gymnoascus reessii by Baranetzky (1872) numerous species of Gymnoascaceae have been proposed, and, as was pointed out recently by Kuehn (1955a), the taxonomy of the family now is rather in a state of chaos. There is considerable confusion at the species and even at the genus level, and only a detailed comparative analysis of a large series of strains of living species coupled with a study of type material will bring order to our understanding of the group as a whole. It is hoped that the present paper will clear up some of the confusion at the generic level.

What taxonomic significance, if any, is to be attached to the imperfect stages encountered in the Gymnoascaceae is not apparent. Species of *Byssochlamys* are characterized by a penicillate conidial apparatus of the *Paecilomyces* type (Raper and Thom, 1949, p. 69), and one species, *B. nivea* Westl. (1909), produces aleuriospores (Pl. I, figs. 2-3) very similar to the thallospores reported for *Eremascus albus* Eidam by Harrold (1950, p. 134). Species of *Myxotrichum, Arthroderma*, etc. commonly produce chlamydospores (arthrospores, aleuriospores) similar to those encountered in certain of the dermatophytes (Nannizzi, 1926). Several forms described as species of *Arachniotus* and *Gymnoascus*, for example *A. ruber* (Van Th.) Schroet. (1893), *A. trachyspermus* Shear (1902; see also Shear, Stevens, and Bain, 1931), and *G. flavus* Klocker (1902), were said to possess a penicillate conidial stage; whether these are to be retained in the Gymnoascaceae or placed in the Eurotiaceae (*Talaromyces* series: C. R. Benjamin, 1955) must await their reisolation and study in pure culture.

The limits of the Gymnoascaceae and the relationship of members of the family to one another and to other simple ascomycetes are uncertain. Usually this complex of fungi is classified near the Eurotiaceae (Eurotiales) where, depending on the point of view, it is considered to be primitive (Gäumann, 1949, p. 107) or advanced (Bessey, 1950, p. 328; Cain, 1956). The writer favors a phylogenetic scheme in which the Gymnoascaceae and the Eurotiaceae are derived from an ancestor perhaps similar to *Eremascus albus* and constitute divergent evolutionary series linked, at present, by such genera as *Arachniotus* of the former family and *Talaromyces* of the latter; the Gymnoascaceae may well represent an evolutionary blind alley.

The purpose of this paper is to describe a new genus of Gymnoascaceae, and, for comparison, to give a brief illustrated summary of the other genera. The family may be characterized as follows:

GYMNOASCACEAE Barantezky, Bot. Zeit. 30:158. 1872.

Ascocarp roundish, usually a cleistothecium consisting of a lax network of interwoven, often anastomosed, thin- or thick-walled hyphae surrounding the ascigerous tissue, or rarely the latter devoid of a special hyphal investment. Peridial hyphae, when present, smooth-walled or roughened, simple or giving rise to variously modified branches or appendages. Asci irregularly disposed, globoid to pyriform, 8spored, wall evanescent. Ascospores one-celled, globose, oblate, ovoid, or lenticular, smooth or sculptured. Asexual reproduction by conidia or chlamydospores.

Type genus: Gymnoascus Baran.

A KEY TO THE GENERA:

Α.	Peridial hyphae thin-walled, similar to vegetative hyphae, or absentB.		
AA.	ridial hyphae thick-walled, conspicuously different m vegetative hyphaeD.		
	B. Peridial hyphae absentByssochclamys (p. 303)		
	BB. Peridial hyphae thin-walled, similar to vegetative hyphaeC.		
C.	Ascospores colorless or light-coloredArachniotus (p. 305)		
CC.	Ascospores brown or brown-violet		
	D. Peridial hyphae uniform, without spine-like branches or other appendagesPseudogymnoascus (p. 315)		
	DD. Peridial hyphae bearing spine-like branches or other appendagesE.		
E.	Appendages not conspicuously different from peridial hyphae; consisting of short spines or blunt projectionsF.		

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EE.	E. Appendages well-defined; often unlike peridial hyphaeG.		
	F.	Peridial hyphae anastomosed; forming a well- defined net	
	FF.	Peridial hyphae not anastomosed; forming a bramble-like aggregateEidamella (p. 311)	
G.	Appendages consisting of slender elongate hyphae forming close spirals		
GG.	Appendages not in the form of spiralsI.		
	H.	Peridial hyphae composed of uniform, more or less symmetrical, dumbbell-shaped cells; append- ages fewArthroderma (p. 305)	
	HH.	Peridial hyphae disarticulating; cells very irregu-	
Ι.	App	endages simple, nearly straight or inrolled apically Myxotrichum (p. 315)	
II.	Арре	endages ctenoidCtenomyces (p. 307)	

BYSSOCHLAMYS Westling, Svensk Bot. Tidskr. 3:134. 1909.

Ascocarp consisting of a more or less globose cluster of asci without any special hyphal investment. Asci globose, 8-spored. Ascospores ovoid, smooth-walled, hyaline. Imperfect stage of the *Paecilomyces* type; broadly clavate aleuriospores present or absent.

Type species: Byssocchlamys nivea Westl. (Plate I)

The simple ascocarp characteristic of this anomalous genus (Pl. I, fig. 1) suggests for it, as was pointed out by Westling (1909), a position intermediate between the Endomycetaceae and the Gymnoascaceae; the similarity between the aleuriospores of *Byssochlamys nivea* (Pl. I, figs. 2-3) and the thallospores of *Eremascus albus* has been mentioned above (p. 302). The penicillate conidial apparatus of *Byssochlamys* (Pl. I, figs. 5-6) would seem to indicate a close relationship of the genus to certain genera of the Eurotiaceae. *Byssochlamys* produces an extensive system of ascogenous hyphae and croziers (Pl. I, fig. 2) similar to that found in many of the Gymnoascaceae and Eurotiaceae (C. R. Benjamin, 1955; Delamater, 1937a; Kuehn, 1955 a, b). Following the suggestion of Kuehn (1955a, p. 542) *Byssochlamys* is here included in the Gymnoascaceae.

Arachniotus trisporus was described by Hotson in 1936, and Rosenbaum later (1944) made a detailed study of its development. This species is characterized by the production of small more or less naked aggregates of asci, relatively large clavate aleuriospores, and a conidial phase of the *Paecilomyces* type. Rosenbaum found that the species grows best at a temperature of between $30^{\circ}-35^{\circ}$ C.

Several cultures received from the Northern Utilization Research Branch, Peoria, Ill., (NRRL 1678, 2205, A-3262, and A-3849) conform to the description given by both Hotson and Rosenbaum for *A. trisporus*. The characteristics of this fungus, including the high optimum temperature of growth, are essentially the same as those given by Westling (1909) in his description of *Byssochlamys nivea*, and *Arachniotus trisporus* is here considered to be a synonym of Westling's species. Cain (1956, p. 140) recognized that *A. trisporus* and *Byssochlamys* are congeneric and proposed the new combination *B. trisporus* (Hots.) Cain.

The type strain of *Byssochlamys fulva* Olliver and Smith (1933; NRRL 1125) has been examined. This species differs from *B. nived* in the more slender elongate conidia (Pl. I, fig. 6), slightly larger ascospores, and the absence of aleuriospores.

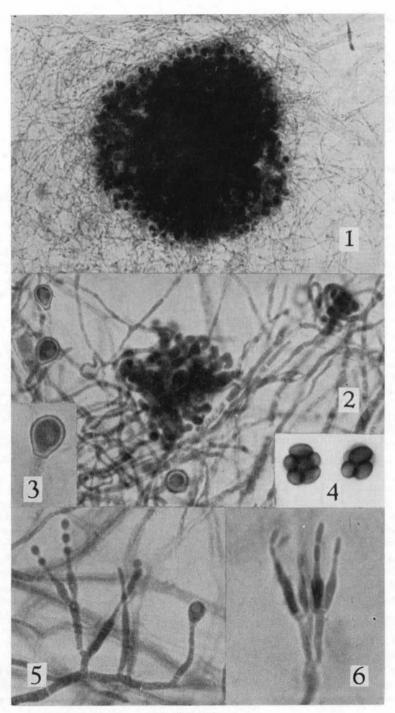


PLATE I.

AMAUROASCUS Schroet., in Cohn, Krypt.-Fl. Schles. 3(2):211. 1893.

ARACHNIOTUS Schroet., ibid., 3(2):210. 1893.

Cleistothecia composed of loosely interwoven, thin-walled, nearly uniform, lightcolored hyphae. Asci 8-spored. Ascospores globose, oblate, ovoid, or ellipsoid, light colored in Arachniotus, brown or brown-violet in Amauroascus.

Type species: Amauroascus niger Schroet.

Arachniotus candidus (Eidam) Schroet.

These genera were established by Schroeter (1893) to accommodate certain forms previously described as species of Gymnoascus by Eidam (1886; G. aureus, G. candidus, and G. verrucosus) and Van Tieghem (1877; G. ruber).

In Schroeter's treatment of Amauroascus two species were considered, A. niger Schroet, and A. verrucosus (Eidam) Schroet. The writer has not seen either of these species, and except for Dangeard's work on the development of the ascocarp of A. verrucosus (1907, pp. 98-105) and Raillo's report of the occurrence of A. niger in soil in the U.S.S.R. (1928) nothing additional apparently has appeared in the literature concerning the genus. If further study should reveal that there are no major characters other than spore color which may serve to distinguish Amauroascus and Arachniotus then it would seem unnecessary to retain both names.

Arachniotus, when established originally (Schroeter, 1893), included three species, A. candidus (Eidam) Schroet., A. aureus (Eidam) Schroet., and A. ruber (Van Th.) Schroet. Several species have been added subsequently including A. citrinus Massee and Salmon (1902), A. trachyspermus Shear (1902), A. terrestris Raillo (1928), and A. dankaliensis (A. Cast.) Beyma (1942).

Plate II illustrates a species of Arachniotus which the writer isolated from rodent dung collected near Claremont, Calif., in Nov. 1953, and which has been maintained in culture since that time (RSABG No. 202). Because of the author's lack of definitive knowledge of other members of the genus no attempt is made here to place this fungus specifically. It does, however, illustrate the characteristics of the genus as laid down originally by Schroeter.

The nearly colorless ascocarp is composed of loosely interwoven, thin-walled, nearly uniform hyphae many of which are spirally coiled distally (as in A. aureus) (Pl. II, figs. 1 and 5). The ascospores are pale yellow, oblate, smooth-walled, with a shallow equatorial groove (Pl. II, fig. 4). Broadly clavate chlamydospores are produced, though not in abundance (PI. II, fig. 2). The ascocarp is initiated by a relatively robust coil (Pl. II, fig. 3).

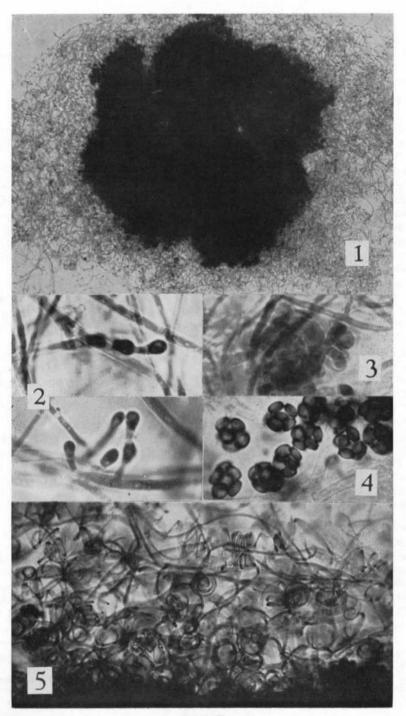
ARTHRODERMA Berkeley, Outlines of British Fungology, p. 357. 1860.

Cleistothecia whitish to pale yellow, globose. The peridium consisting of a network of branched, anastomosed, nearly hyaline hyphae composed of thick-walled, minutely and densely asperulate, constricted, symmetrical or asymmetrical, dumbbell-shaped cells; a few slender, elongate, thin-walled, septate, spiral appendages produced terminally or laterally; free ends numerous. Asci globose, 8-spored. Ascospores yellow in mass, small (2.4-3.3 μ X 2 μ), smooth, appearing, by phase con-

PLATE I.

Conidiophore showing characteristic elongate condia. x 1230.

Figs. 1-5. Byssochlamys nivea. Fig. 1. Mature ascocarp. x 345. Fig. 2. Ascocarp initial (upper right); immature ascocarp showing croziers (center); aleuriospores (bottom and upper left). x 940. Fig. 3. Aleuriospore. x 1330. Fig. 4. Ascospores. x 1330. Fig. 5. Conidiophore showing typical ovoid conidia; note aleuriospore at right. x 980. Fig. 6. Byssochlamys fulva.



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trast, to possess a slight equatorial groove. Clavate aleuriospores produced in abundance by the vegetative hyphae.

Type species: Arthroderma curreyi Berk. (Plates III and IV)

The type, and only known species, *Arthroderma curreyi*, has masqueraded in the literature as the perfect phase of *Ctenomyces serratus* ever since Eidam described the latter in 1880.

Currey first reported this fungus in 1854, but he did not describe it and stated merely "if a new genus be constituted for it, I think that, from the jointed nature of the hairy covering, 'Arthroderma' would be an appropriate name". Arthroderma was validated by Berkeley six years later when he adopted the name suggested by Currey. Currey's brief mention of the fungus in question was accompanied by a figure, and because of the unique character of the peridial hyphae of *A. curreyi* there can be little or no doubt that he actually studied this species.

Arthroderma curreyi appears to be rather common, and it has been reported a number of times in the liteurature as *Ctenomyces serratus* (Dangeard, 1907; Eidam, 1880; Smith, 1903; Grove, 1922; Marsh, 1926; Nannizzi, 1926). The fungus is found most frequently on rotting feathers, but it has been reported on other types of offal as well. Smith (1904), with reference to Salmon (1900), called attention to the fact that *A. curreyi* and Eidam's *C. serratus* are the same.

In his original description of *C. serratus* Eidam described not only an ascigerous stage (*A. curreyi*) but also what he believed to be a resting or sclerotial stage bearing conspicuous comb-like appendages (Pl. V, figs. 1-2). This "resting stage" has not been reported in subsequent accounts of *C. serratus*, and Eidam's interpretation of it has been accepted through the years (Gäumann, 1949, p. 107); its true nature is discussed in the next section. The development of *Arthroderma curreyi* (as *C. serratus*) was discussed by Eidam in his original paper (1880), by Matruchot and Dassonville (1899), and by Dangeard (1907, pp. 86-97).

Material examined: Cambridge, Mass., 10 Nov., 1951, R. K. Benjamin, on feathers of dead bird (culture, RSABG No. 186); In Farlow Herbarium*; Cambridge, Mass., 1896-97, Thaxter No. 183, on feathers; Cambridge, Mass., 1900, Thaxter No. 219, on old horn; Panama, Oct., 1916, Thaxter No. 216, on feathers; Kittery Point, Me., Aug., 1926, Thaxter No. 300, No. 506, on buried manure in garden. Exsiccati: Rhem, Ascomyceten, No. 1625.

CTENOMYCES Eidam, in Cohn, Beitr. Biol. Pfl. 3:274. 1880.

Cleistothecia orange-brown, globose, about 100-350 μ in diameter, excluding the appendages. Peridium composed of a thin layer of densely interwoven, slender, pale orange, thin-walled hyphae surrounded by a lax network of anastomosed, thick-walled septate (slightly swollen), asperulate, orange-brown hyphae, 3.3-6 μ in diameter, which give rise to numerous curved, septate, ctenoid appendages. Appendages 100-150 μ long consisting of about 5-11 thick-walled asperulate cells; each cell, above the more elongate basal one or two cells, growing outward distally on one side

PLATE II.

^{*}The collections of Gymnoascaceae on deposit in the Farlow Herbarium, Harvard University, Cambridge, Mass., were examined during the tenure of the author as a National Research Fellow in Botany, 1951-52; the author is indebted to the late Dr. W. Lawrence White for permission to study this material.

Figs. 1-5. Arachniotus sp. Fig. 1. Mature ascocarp. x 120. Fig. 2. Chlamydospores. x 1300. Fig. 3. Ascocarp initial showing early stages in the development of ascogenous hyphae. x 930. Fig. 4. Ascospores. x 1300. Fig. 5. Margin of ascocarp showing coiled peridial hyphae. x 560.

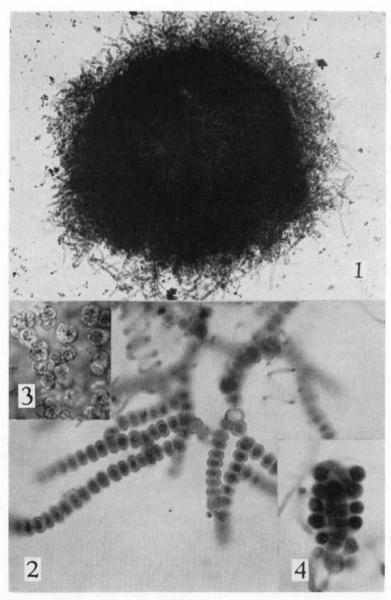


PLATE III.

Figs. 1-4. Arthroderma eurreyi. Fig. 1. Mature ascocarp. x 105. Fig. 2. Peridial hyphae. x 625. Fig. 3. Ascospores. x 1300. Fig. 4. Asccarp initial showing ascogonium coiled around the elongate antheridium. x 1300.

PLATE IV.

Figs. 1-5. Artbroderma curreyi. Fig. 1. Two mature ascocarps. x 105. Fig. 2. Portion of peridial hypha showing asperulate dumbbell-shaped cells. x 1300. Fig. 3. Coiled appendage. x 1300. Fig. 4. Vegetative hyphae bearing aleuriospores; note dense aggregate of spore-bearing hyphae at right. x 560. Fig. 5. Aleuriospores; these are asperulate over the distal surface. x 1300.

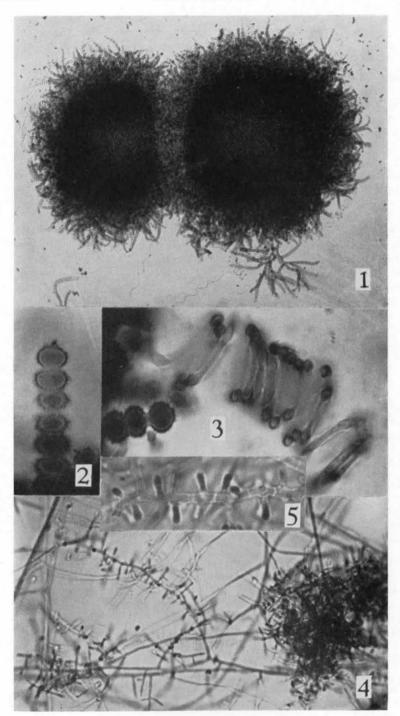


PLATE IV.

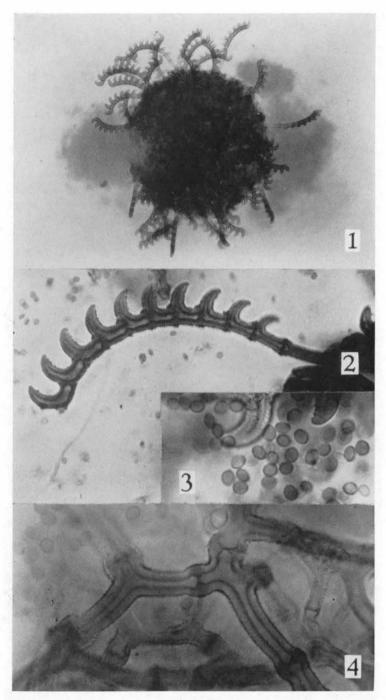


PLATE V.

to form a recurved, accuminate, tooth-like protuberance. Ascospores pale orange in mass, slightly lenticular, more convex on one side, 2-2.6 μ X 3.3-3.6 μ .

Type species: Ctenomyces serratus Eidam (Plate V)

As was pointed out in the preceding section, Eidam's description of *C. serratus* (1880) included what he thought represented two separate phases of a single species. One, the presumed perfect stage, has been shown to be identical to *Arthroderma curreyi* Berk.; the other, considered by Eidam to be a resting or sclerotial phase, is characterized especially by the production of a unique type of ctenoid appendage (Pl. V, figs. 1-2). Although several students have collected, discussed, and illustrated the supposed sexual stage of *C. serratus* (i.e. *A. curreyi*) since Eidam described it, no one appears to have reported the sclerotial stage.

In the Thaxter collection, on deposit in the Farlow Herbarium, several collections of the presumed resting phase of C. servatus have been examined by the writer, and a study of this material reveals that it represents a gymnoascaceous fungus quite distinct from A. curreyi. It is apparent that Eidam's feather was supporting the growth of two different members of the Gymnoascaceae, and, for some reason, he was led to believe that these were but the perfect and a sclerotial phase of the same species.

Ctenomyces serratus Eidam is to be retained as the name of the fungus which Eidam's resting phase represents; this name is derived from the comb-like structure of the appendages characteristic of the species, and its retention should result in no confusion.

Material examined: In Farlow Herbarium: Arlington, Mass., date ?, Thaxter No. 173, on feathers; Cambridge, Mass., date ?, Thaxter No. 217, on feathers; Soledad, Cuba, 1903-04, Thaxter No. 166, on feathers; Panama, Oct. ,1916, Thaxter No. 175, No. 188, on feathers; Liberia, Africa, Sept., 1896, Thaxter No. 312, on ass dung.

EIDAMELLA Matruchot and Dassonville, Bull. Soc. Myc. Fr. 17:129. 1901.

Ascocarps roundish, composed of a radiating bramble-like aggregate of blackish, thick-walled, septate hyphae bearing numerous short, septate, apiculate, more or less deflexed branchlets; many of the hyphae surrounding the central ascigerous mass bearing one or more short, hyaline, spiral branchlets terminally. Asci globose to ovoid, pedicellate, evanescent. Ascospores nearly hyaline, lenticular, delicately striate with minute longitudinal furrows.

Type species: *Eidamella spinosa* Mat. and Dass. (Plate VI)

Matruchot and Dassonville isolated *E. spinosa* from a lesion on the diseased skin of a dog, and the species was found to grow readily in culture on a variety of media; its morphology, development, and pathogenic character were discussed in some detail. DeLamater (1937b) published an account of the development of a fungus determined as *E. spinosa* which Dr. N. F. Conant had isolated from a diseased fingernail. This strain was deposited in the Centraalbureau at Baarn, and it has been obtained and studied by the writer. The author also has isolated two strains of a species which are identical in all regards to the one studied by DeLamater, and, in addition, he has examined preserved material on deposit in the collections of the Farlow Herbarium which appears to represent the same species.

PLATE V.

Figs. 1-4. Ctenomyces serratus. Fig. 1. Mature ascocarp. x 115. Fig. 2. Appendage. x 560. Fig. 3. Ascospores. x 1300. Fig. 4. Thick-walled peridial hyphae. x 1300.

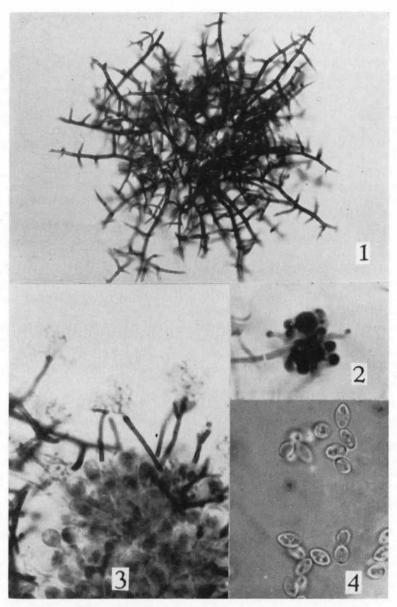


PLATE VI.

Figs. 1-4. Eidamella deflexa. Fig. 1. Mature ascocarp. x 335. Fig. 2. Ascocarp initial. x 1300. Fig. 3. Crushed ascocarp showing asci and peridial hyphae bearing terminal groups of spiral branchlets. x 645. Fig. 4. Ascospores. x 1300.

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In their original description of *E. spinosa* Matruchot and Dassonville gave the dimensions of the asci as 3-4 μ wide by 6-7 μ long and of the ascospores as 1.5 μ wide by 3 μ long. DeLamater lists similar measurements for the strain which he studied, but he does give 10 μ as an upper limit for the length of the asci. In all seven of the strains of *Eidamella* studied in the course of this work, including DeLamater's, the dimensions of the ascospores have been found to be consistently larger than those given by the above authors. The ascospores are nearly hyaline, pale orange-yellow in mass, lenticular, 2.6-2.9 μ X 4.6-5.2 μ , and delicately striate with minute longitudinal furrows. The last feature seems not to have been noticed previously. The asci have been found to measure about 7-9 μ X 13-18 μ (including pedicle).

Recently Saccas (1950) described a species of *Eidamella*, *E. papyricola*, which was found growing saprophytically on paper (the pages of a book). This species is distinguished from *E. spinosa* chiefly on the basis of the fact that the dimensions of the asci and ascospores are larger than those given by Matruchot and Dassonville for *E. spinosa*. Saccas lists 15-16 μ X 7-9 μ as average for the asci of *E. papyricola* and 2-3.5 μ X 4-6 μ (average 3 μ X 5.1 μ) for the ascospores.

The original biogenous strain of *E. spinosa* studied by Matruchot and Dassonville no longer is available, and the writer has not seen Saccas' strain of *E. papyricola*. Of the seven strains of *Eidamella* studied by the writer six originally were found growing as saprophytes and one as a parasite. A study of the published data of Matruchot and Dassonville for *E. spinosa* and Saccas for *E. papyricola* reveals that other than a discrepancy in ascus and ascospore dimensions the species are essentially the same, and they are here considered as probably synonymous.

Eidamella spinosa undoubtedly is synonymous with Myxotrichum deflexum Berkeley (1838). Berkeley, who rarely bothered to illustrate any of the fungi which he described, figured this species, and his drawings would suggest that his fungus and the one described by Matruchot and Dassonville are congeneric. A specimen of *M. deflexum* in Rabenhorst's Fungi europaei (No. 2464) was collected in 1874 by C. E. Broome, associate of Berkeley, and it is identical to the various collections considered to represent *E. spinosa* which have been studied by the writer. The characteristics of this species are such that it does not fit the current concept of the genus Myxotrichum and, for the present at least, it is felt that the genus Eidamella should be retained. The species described by Matruchot and Dassonville accordingly is here renamed:

Eidamella deflexa (Berkeley) n. comb.

Myxotrichum deflexum Berkeley, Ann. Nat. Hist.; or Mag. Zool, Bot., and Geol. 1:260. 1838.

Material examined: Belmont, Mass., March, 1952, R. K. Benjamin, on rotting board in basement (culture, RSABG No. 57); LaVerne, Calif., 22 Dec., 1953, R. K. Benjamin, on rotten rug in yard (culture, RSABG No. 203); DeLamater's strain in Centraalbureau voor Schimmelcultures, Baarn (culture, RSABG No. 58). In Farlow Herbarium: West Roxbury, Mass., date ?, Piguet; Lavallol, Argentina, 1906-07, Thaxter No. 5311, on feathers. Exsiccati: Ellis and Everhart, Fungi columbiani, No. 1360 (as Myxotrichum chartarum Kze.); Rabenhorst, Fungi enropaei, No. 2464 (as M. deflexum Berk.).

Datta (1932) reported a fungus which had been isolated from the diseased skin of a dog, and the name *Eidamella actoni* was suggested for it. Datta did not accompany this name with a formal description and measurements were not given. The species reportedly produces asci with more than eight ascospores.

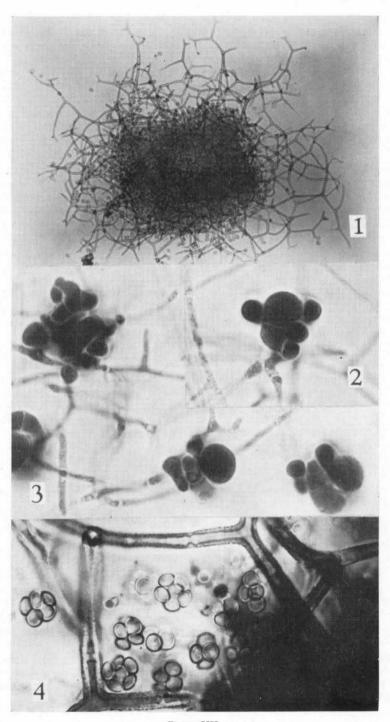


PLATE VII.

GYMNOASCUS Brantezky, Bot. Zeit. 30:158. 1872.

Ascocarp composed of a network of branched, anastomosed, thick-walled, septate, smooth or asperulate hyphae with many radiating free ends; the latter spine-like or more or less elongate septate branches bearing short, apiculate or blunt, straight or curved branchlets laterally. Asci globoid, 8-spored, evanescent. Ascospores globose, oblate, or lenticular, smooth or variously sculptured.

Type species: Gymnoascus reessii Baran. (Plate VII)

Baranetzky, in establishing the Gymnoascaceae (1872), described and gave an admirable account of the development of *G. reessii* which he had found growing on the dung of horse and sheep. A vague generic concept led contemporary students to include in *Gymnoascus* a number of different, though related, fungi, and several of these later were transferred to other genera (Schroeter, 1893). Excluding those which have been placed in other genera, some thirteen species of *Gymnoascus* are listed in Saccardo (1889, 1892, 1895, 1899, 1902, 1906, 1910, and 1928), and few of these are known from other than their original, often brief and unillustrated, descriptions. Until a thorough monographic study of the group is undertaken the status of many of the species of *Gymnoascus* which have been named is uncertain.

Gymnoascus reessii appears to be common, and a number of strains have been isolated by the writer which correspond in all respects to the description of it given originally by Baranetzky, and later by Dale (1903). Only three isolates have been obtained thus far which the author regards as species of Gymnoascus other than G. reessii.

Material examined: *Gymnoascus reessii*. Urbana, Ill., Sept., 1948, R. K. Benjamin, on goat dung (culture, RSABG No. 60; NRRL A-3612); Belmont, Mass., March, 1952, R. K. Benjamin, on rat dung (culture, RSABG No. 61); San Gabriel Mts., San Bernardino Co., Calif., R. K. Benjamin, June, 1953, on horse dung (culture, RSABG No. 184), Nov., 1953, on rodent dung (culture, RSABG No. 185), Nov., 1953, on coyote dung (culture, RSABG No. 201); Big Pines, Los Angeles Co., Calif., Nov., 1953, R. K. Benjamin, on deer dung (culture, RSABG No. 205); Mt. San Antonio, San Gabriel Mts., Los Angeles Co., Calif., Sept., 1955, R. K. Benjamin, on coyote dung (culture, RSABG No. 404).

PSEUDOGYMNOASCUS Raillo (1928) is known to the writer only through the description given by Gilman (1945, pp. 148-149). The genus was established to include species which resemble *Gymnoascus* except that the thick-walled peridial hyphae are without the spine-like branches which characterize the latter genus. A specimen in Sydow's Mycotheca marchcica, No. 4031, determined as *Arachniotus candidus*, possibly belongs here, as does a specimen in the Thaxter collection of Gymnoascaceae at Harvard, No. 2611, Maraval Valley, Trinidad, 1912-13, on a large roach, determined as *Gymnoascus* sp. In both of these the peridium consists entirely of a dense network of colorless, anastomosed, thick-walled hyphae.

MYXOTRICHUM Kunze, Myk. Hefte II:108. 1823.

Ascocarp composed of a network of branched, anastomosed, thick-walled, septate, smooth or asperulate hyphae; free ends usually numerous, forming short spines and elongate, septate or non-septate, straight, curved, or uncinate appendages. Asci glo-

PLATE VII.

Figs. 1-4. Gymnoascus reessii. Fig. 1. Mature ascocarp. x 170. Figs. 2-3. Ascocarp initials; the one at the upper left beginning to form croziers. x 1300. Fig. 4. Peridial hyphae and ascospores. x 1300.

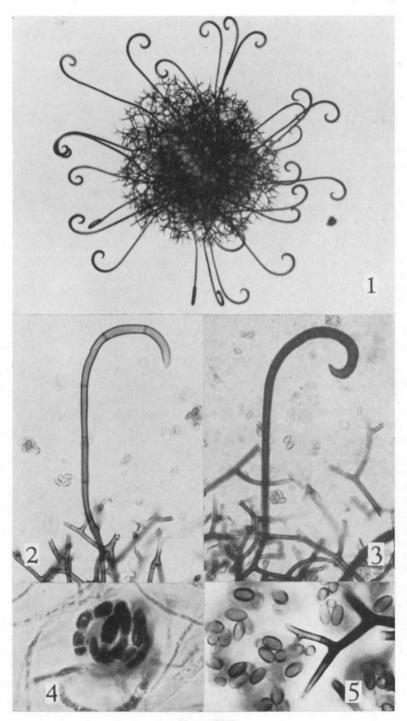


PLATE VIII.

GYMNOASCACEAE

boid, 8-spored, evanescent. Ascospores globose, oblate, or ovoid, smooth or variously sculptured.

Type species: Myxotrichum chartarum Kze. (Plate VIII)

Since the description of *Myxotrichum chartarum* Kze. and *M. murorum* Kze. (Kunze and Schmidt, 1823) numerous species of *Myxotrichum* have been named. Saccardo lists more than twenty species in his Sylloge Fungorum (1886, 1892, 1895, 1906, and 1911), and several have been characterized more recently (Robak, 1932; Kuehn, 1955a, 1955b). As in the case of *Gymnoascus* many of the species of *Myxotrichum* which have been proposed are known only from their original, often very brief, descriptions.

The writer has isolated or obtained from other collectors about twenty strains of *Myxotrichum* representing several species. Two of these, *M. chartarum* and *M. uncinatum* (Eidam) Schroet. (1893), are illustrated here (Plates VIII and IX). These species are examples of two distinct types which are included in the genus, and on the basis of marked differences in the nature of the ascocarp initials, appendages, ascospores, and chlamydospores it would seem that they probably are not too closely related.

The ascocarp of the strain of *M. chartarum* studied here (RSABG No. 55) is globose, about 150-350 μ in diameter, exclusive of the appendages, and it consists of a network of branched, anastomosed, smooth, thick-walled, septate, brownish-black to nearly black hyphae, 1.7-3.3 μ in diameter, with many radiating, short, spine-like free ends and long uncinate appendages. The latter are about 50-175 μ long, smoothwalled, 6- to 9-septate, about 2.4-3.3 μ in diameter at the base, with their diameter increasing gradually to about 4.5-6 μ near the acute inrolled apex. Ascospores orange-brown, ovoid, 2.4-2.6 μ X 4.3-5.2 μ , delicately striate with minute longitundinal furrows. Clavate, doliform, or oblong, intercalary or terminal, solitary or seriate chlamydospores about 1.3-3.3 μ X 3.2-8 μ are formed in the aerial vegetative mycelium.

Several of the described species of *Myxotrichum* are characterized by the production of septate appendages which, as in *M. aeruginosum* Mont. (Montagne, 1836; see also Peyronel, 1914) and *M. spinosum* Massee and Salmon (1902, p. 64), may be nearly straight or, as in *M. chartarum* and *M. carminoparum* Robak (1932), uncinate. The writer obtained a culture of Robak's strain of *M. carminoparum* from the Centraalbureau voor Schimmelcultures in 1950, but all attempts to induce it to produce ascocarps in culture have failed. According to Robak's description *M. carminoparum* differs from *M. chartarum* chiefly in the smaller cleistothecia and uniform, not apically enlarged, appendages.

Myxotrichum uncinatum (Pl. IX) is representative of a second group of species of Myxotrichum, including M. johnstoni Massee and Salmon (1902, p. 64), M. emmonsii Kuehn (1955a), M. thaxteri Kuehn, and M. conjugatum Kuehn (1955b), in which the appendage is unicellular. In the strain of M. uncinatum studied here, discussed recently in some detail by Kuehn (1955a), the red-brown to orangebrown ascocarp (Pl. IX, fig. 1) is composed of a network of thick-walled, anastomosed, septate, asperulate hyphae with a few blunt, spine-like free ends and many elongate, nearly uniform, non-septate, uncinate appendages (Pl. IX, fig. 2); the

PLATE VIII.

Figs. 1-5. Myxotrichum chartarum. Fig. 1. Mature ascocarp. x 160. Fig. 2. Immature appendage; note septa. x 625. Fig. 3. Mature appendage. x 625. Fig. 4. Ascocarp initial. x 1300. Fig. 4. Ascospores and spine-like free ends of peridial hyphae. x 1300.

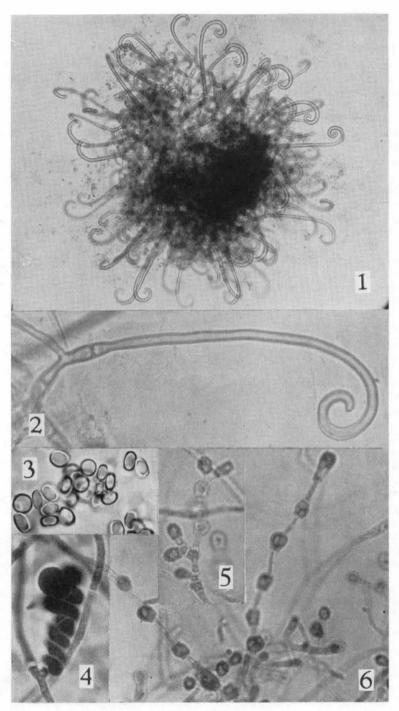


PLATE IX.

June, 1956]

ascospores are pale orange-brown, smooth, oblate (Pl. IX, fig. 3); the imperfect phase consists of terminal or intercalary, asperulate, short-clavate chlamydospores (Pl. IX, figs. 5-6). The ascocarp initials produced by this strain of *M. uncinatum* appear to be very similar to those figured by Eidam when he described this species as *Gymnoascus uncinatus* (compare Pl. IX, fig. 4, with Eidam's fig. 34, Pl. XIV 1880).

Material examined: *Myxotrichum chartarum*. Belmont, Mass., March, 1952, R. K. Benjamin, on rotting board in basement (culture, RSABG No. 55). In Farlow Herbarium: Kittery Point, Me., July, 1930, Thaxter No. 5347, on tarred paper. Exsiccati: Flora exsiccata Austro-Hungarica, No. 3180; Rabenhorst, Fungi europaei, No. 1169; Berkeley, British fungi, Fasc. III, No. 207. *Myxotrichum uncinatum*. Urbana, Ill., March, 1949, R. K. Benjamin, on dung (culture, RSABG No. 56; NRRL A-3610). In Farlow Herbarium: Sharon, Mass., Oct., 1916, Piguet, on bones in hen house; New Haven, Conn., date ?, Thaxter No. 509, on hen's dung, No. 591, on dog's dung.

Shanorella gen. nov.

Cleistotheciis globosis aut ovoideis, parvis, aggregatis; peridio ex reticulo laxo hypharum septatarum parietibus crassis composito; hyphis maturis facile disarticulatis; cellulis plus aut minus elongatis, rectis aut curvatis, simplicibus aut ramosis, inaequalibus, appendicula spiralia hyphis elongatis septatis gerentibus; ascis octosporis, evanidis; ascosporis luteis, oblatis.

Etym: Named for Dr. Leland Shanor, Mycologist.

Cleistothecia globoid or ovoid, small, aggregated; peridium composed of a lax network of thick-walled septate hyphae readily disarticulating at maturity; the cells more or less elongate, straight or curved, simple or branched, very irregular in size and shape, giving rise to coiled appendages composed of slender, elongate, septate hyphae; asci 8-spored, evanescent; ascospores yellow, oblate.

Shanorella spirotricha sp. nov. (Plates X, XI, and XII)

Cleistotheciis globosis aut ovoideis, luteis aut aureis, aggregatis, saepe plus aut minus continuis, parvis, ca. 100-200 μ diam., appendiculis exclusis. Peridii hyphis flavis, septatis, laevibus, crasso-parietalibus, in aetate disarticulatis; cellulis plus aut minus elongatis, ca. 3-15 μ latis, 10-35 μ longis, rectis aut curvatis, simplicibus aut ramosis, inaequalibus; parietibus 0.65-2 μ crassis; appendiculis numerosis, angustis (1-1.3 μ latis), hyalinis, septatis, aequalibus, terminalibus aut lateralibus, parietibus tenuibus, spiralia stricte voluta 10-20 μ lata, 25-40 μ longa faciendis. Ascis hyalinis, globosis, 5.2-7.8 μ diam., octosporis. Ascosporis luteis, compresso-oblatis, 3.5-3.9 μ X 2 μ , laevibus, parte lata elevata equatoriale asperulaque. Chlamydosporis 2-3.3 μ X 3.3-12 μ , hyalinis, terminalibus, lateralibus aut intercalaribus, clavatis aut oblongis.

Cleistothecia globoid or ovoid, bright-yellow to golden-yellow, clustered, often forming a dense more or less continuous aggregate, small, about 100-200 μ in diameter, not including the coiled appendages. Peridium composed of pale-yellow, septate, thick-walled, smooth hyphae; peridial hyphae becoming disarticulated at maturity; the cells more or less elongate, about 3-15 μ wide by 10-35 μ or more long, straight or curved, simple or branched, very irregular in size and shape; the cell-wall 0.65-2 μ thick; appendages numerous, consisting of slender (1-1.3 μ

PLATE IX.

Figs. 1-6. Myxotrichum uncinatum. Fig. 1. Mature ascocarp. x 155. Fig. 2. Mature appendage.
x 500. Fig. 3. Ascospores. x 1300. Fig. 4. Ascocarp initial showing mutually coiled equal gametangia. x 1300. Figs. 5-6. Chlamydospores. x 950.

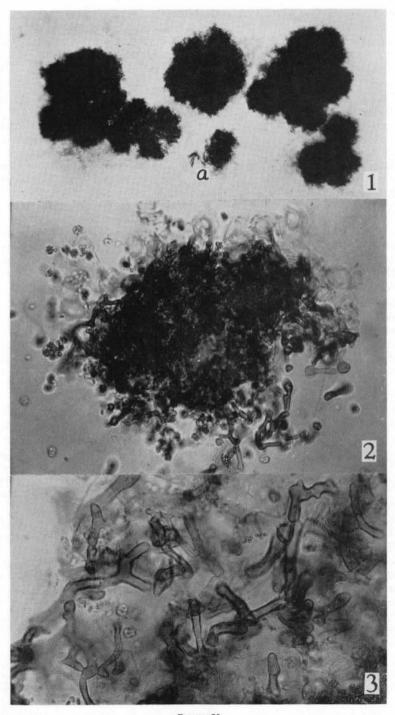


PLATE X.

wide), thin-walled, hyaline, septate, uniform terminal or lateral outgrowths of peridial cells forming closely wound coils of 20-30 turns more or less; coils about 10-20 μ wide by 25-40 μ long. Asci hyaline, globoid, 5.2-7.8 μ in diameter, 8-spored, the wall evanescent. Ascospores bright yellow, flattened-oblate, about 3.5-3.9 μ in diameter in polar view by 2 μ wide in equatorial view, smooth except for a broad, slightly elevated, roughened equatorial band. Imperfect phase consisting of hyaline, terminal, lateral, or intercalary, clavate or oblong chlamydospores, 2-3.3 μ X 3.3-12 μ .

The origin of the three isolates representing this species which are maintained in the culture collection of the Rancho Santa Ana Botanic Garden is as follows: RSABG No. 64—on rabbit fur in moist chamber culture, Urbana, Champaign Co., Ill., March, 1949; RSABG No. 65—on chicken feathers in moist chamber culture, Farina, Fayette Co., Ill., Sept., 1950; RSABG No. 156 (TYPE)—on feathers of dead bird in moist chamber culture, Claremont, Los Angeles Co., Calif., Dec., 1953. Dried material representing each of these strains has been placed in the herbarium of the Botanic Garden and in the Farlow Herbarium, Harvard University. Transfers have been deposited in the culture collections of the American Type Culture Collection, Washington, D. C., the Centraalbureau voor Schimmelcultures, Baarn, Netherlands, and the Northern Utilization Research Branch, Peoria, Ill.

The character which distinguishes this genus most readily from all other known genera of the Gymnoascaceae is the nature of the peridial hyphae. When the ascocarp is mature the thick-walled hyphae of which it is composed tend to disarticulate, and the individual cells present an unending array of sizes and shapes (Pl. X, fig. 3). The coiled appendages (Pl. XI, figs. 2-3) are similar to those produced by *Arthroderma* both in shape and origin.

Colonies of *Shanorella* on YpSs agar* grow rapidly and nearly cover the area of a standard petri-dish within a period of about four weeks. The felt is low-growing relatively close-textured, and white becoming yellow to orange-yellow as cleistothecia mature. Ascocarps are produced in abundance, and each cleistothecium appears to arise from a single robust somewhat irregular coil which becomes separate soon after it is formed (Pl. XII, fig. 1). The resulting ascogonium gives rise to ascogenous hyphae producing croziers (Pl. XII, fig. 2). Vegetative hyphae surrounding the developing ascogonium undergo further differentiation and produce the characteristic thick-walled hyphae composing the peridium (Pl. X, figs. 2-3; Pl. XI, fig. 2). Chlamydospores are produced in considerable numbers even in young vigorous cultures (Pl. XII, figs. 4-5).

Clements and Shear (1931, pp. 48-49) included the following genera in their treatment of the Gymnoascaceae: Amauroascus, Arachniotus, Carpenteles, Conidiascus, Ctenomyces, Diplostephanus, Eidamella, Gymnoascus, Hexagonella, Lilliputia, Myrillium, Myxotrichum, Penicilliopsis, and Rollandina. The following comments may be made regarding those genera listed above which have not been dealt with in the body of this paper:

Carpenteles Langeron (1922) is recognized by C. R. Benjamin (1955) as the

*Emerson, Ralph. 1941. Lloydia 4(2):87.

PLATE X.

Figs. 1-3. Shanorella spirotricha. Fig. 1. A single ascocarp (a) and clusters of ascocarps. x 60. Fig 2. Mature ascocarp. x 350. Fig. 3. Peridial hyphae showing extreme variability in shape of individual cells. x 560.

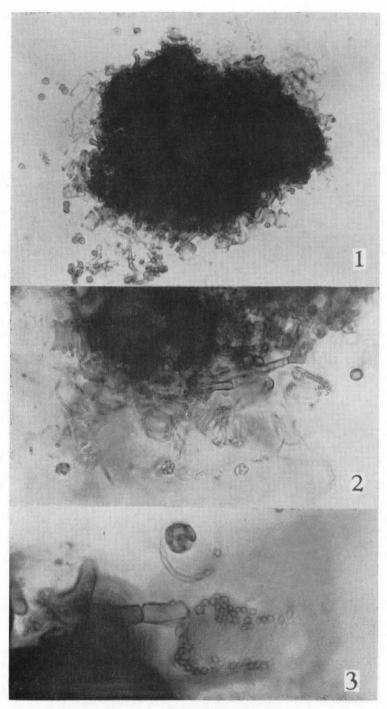


PLATE XI.

valid generic name for the ascosporic stage of those species of *Penicillium* in which the ascocarp wall is sclerotioid or parenchymatous-like. It is placed in the Eurotiaceae.

Conidiascus Holtermann (1898, p. 23), based on C. paradoxus, is questionably assigned to the Endomycetales by Ainesworth and Bisby (1954, p. 84).

Diplostephanus Langeron (1922) was created for the perfect stage of aspergilli of the Aspergillus nidulans type (Thom and Raper, 1945, p. 8). According to C. R. Benjamin (1955) the valid name for the ascosporic stage of these fungi, members of the Eurotiaceae, is *Emericella* Berk. and Br. (Berkeley, 1857, p. 340).

Hexagonella Stevens and Guba (Stevens, 1925, pp. 89-91) is represented by a single species, *H. peleae*, collected in Hawaii. The ascocarp of this fungus consists of an epiphyllous, flat, net-like thallus in which the thick-walled 8-spored asci are borne singly in hexagonal cell meshes. The ascospores are 3-celled, ellipsoid or oblong, obtuse, brown. This fungus would appear to be allied to the Atichiaceae or Saccardiaceae of the Myriangiales (Luttrell, 1951, p. 78).

Lilliputia Boud. and Pat. (1900, pp. 144-146) founded on L. gaillardi, and placed by its authors in the Tuberaceae, has been studied more recently by Dennis and Wakefield (1946, pp. 145-147, fig. 5) who concluded that the fungus might more properly be placed in the Eurotiaceae near Eurotium. They changed the name of species to Lilliputia insignis (Winter) Dennis and Wakefield.

Myrillium myriosporus (Rostrup) Clements (1931, p. 246) is based on Gymnoascus myriosporus Rostrup which is known to the writer only through the brief account of it given by Saccardo (1895, p. 483). This species is said to produce polysporous asci, and because of this fact Saccardo placed it in a separate subgenus, Rostrupiella. Until the fungus is reinvestigated its status is uncertain.

Penicilliopsis Solms-Laubach (1887) is usually included in the Eurotiaceae (Gaumann, 1949, p. 113; Bessey, 1950, p. 356).

Rollandina, represented by a single species, *R. capitata*, was described by Patouillard in 1905. The fungus was collected originally in Tonkin (now North Vietnam) by M. L. Boutan who found it growing on dead plant debris. The material studied by Patouillard had been preserved in a solution of formalin.

Through the kindness of Dr. I. Mackenzie Lamb the type of *R. capitata* in the Patouillard collections in the Farlow Herbarium was sent to the writer for study, and an examination of this material leads to the following emendations or additions to the account of the species given by Patouillard: (a) the hyphae composing the capitulum are densely and minutely asperulate—Patouillard does not mention this fact; (b) the oblate ascospores possess a slightly elevated, broad, equatorial band rather than a shallow groove as stated by Patouillard (Pl. XIII, fig. 1); (c) in addition to the numerous glomerules of asci, the hyphae composing the capitulum also give rise to large, yellow-brown, 5-septate, vertucose, cigar-shaped aleuriospores about 47-61 μ X 9.7-11.9 μ (Pl. XIII, fig. 3-4). These spores are produced singly in lateral outgrowths of the hyphae (Pl. XIII, fig. 2). Patouillard's description of *R. capitata* is emended as follows:

Fruiting structure whitish, consisting of an elongate stipe 15-20 mm. tall by 1 mm. wide, composed of branched, septate, smooth-walled, compacted, more or less parallel hyphae, supporting a subglobose somewhat lobate capitulum 5-8 mm.

PLATE XI.

Figs. 1-3. Shanorella spirotricha. Fig. 1. Mature ascocarp. x 265. Fig. 2. Margin of ascocarp showing coiled appendages. x 560. Fig. 3. Coiled appendage. x 1300.

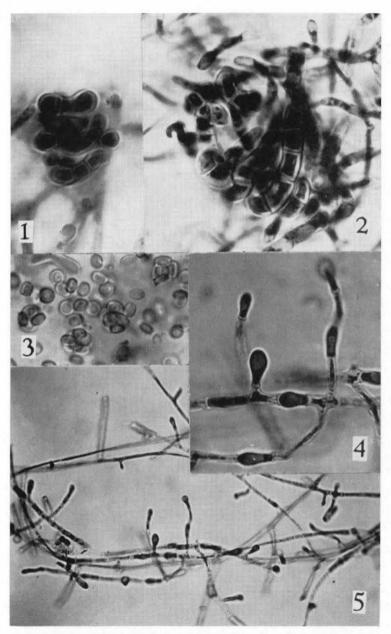


PLATE XII.

Figs, 1-5. Shanorella spirotricha. Fig. 1. Coiled septate ascocarp initial. x 1300. Fig. 2. Young ascocarp showing irregularly coiled ascogonium which is beginning to form ascogenous hyphae; note crozier at left. x 1300. Fig. 3. Ascospores. x 1300. Fig. 4. Typical clavate chlamydospores showing their intercalary, lateral, or terminal position in vegetative hyphae. x 1300. Fig. 5. Vegetative hyphae with chlamydospores. x 560.

in diameter; the latter consisting of an interwoven mass of branched, septate, asperulate hyphae within which are immersed numerous small white glomerules 150-600 μ in diameter; glomerules consisting of a dense aggregate of small, ovoid, 8-spored asci, about 6 μ X 8 μ , surrounded by a thin layer of compact hyphae; ascospores colorless, small, oblate, 3.9-4.6 μ in diameter in polar view by 2.3-2.6 μ in diameter in equatorial view, smooth, with a broad, slightly elevated, equatorial band; large, yellow-brown, 5-septate, vertucose, elongate-ovoid aleuriospores, about

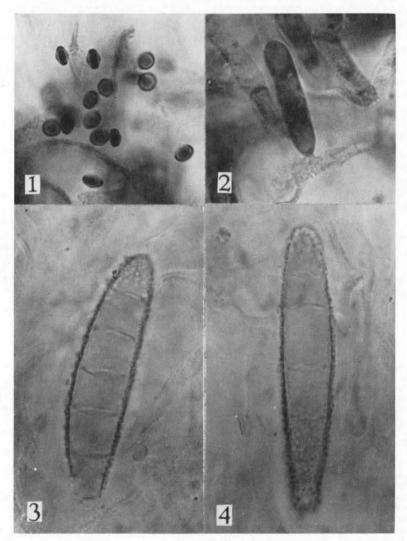


PLATE XIII.

Figs. 1-4. Rollandina capitata. Fig. 1. Ascospores. Fig. 2. Immature aleuriospore showing its lateral origin. Figs. 3-4. Mature aleuriospores; the one shown in Fig. 3 still attached to the parent hypha. All x 1300. 47-61 μ X 9.7-11.9 μ , borne laterally on the hyphae composing the capitulum.

Because of the resemblance of the ascigerous glomerules to the ascocarps of Gymnoascus Patouillard placed Rollandina in the Gymnoascaceae, but in view of the highly developed compound fruiting structure of Rollindina it would seem that the alliance of this genus is with the Onygenaceae rather than the Gymnoascaceae.

SUMMARY

1. A monotypic new genus of the Gymnoascaceae, based on Shanorella spirotricha, is described. This genus is readily distinguished from other known genera included in the family by the character of the peridial hyphae which, at maturity, disarticulate into irregularly shaped thick-walled cells many of which bear conspicuous coiled appendages.

2. The Gymnoascaceae is reviewed and a key to the following genera included in the family is presented: Amauroascus, Arachniotus, Arthroderma, Byssochlamys, Ctenomyces, Eidamella, Gymnoascus, Myxotrichum, Pseudogymnoascus, and Shanorella. A brief discussion of each of the above genera is given, and a representative species of each genus, with the exception of Amauroascus and Pseudogymnoascus, is illustrated.

3. It is shown that the original description of *Ctenomyces serratus* Eidam (1880) included species representing two genera of gymnoascaceous fungi. One of these, Eidam's ascosporic stage, is Arthroderma curreyi Berkeley (1860); the other, considered by Eidam to be a sclerotial phase of his species, is retained under the name used by Eidam.

4. Eidamella spinosa Matruchot and Dassonville (1901) is shown to be synonymous with Myxotrichum deflexum Berkeley (1838). The genus Eidamella is retained, however, and the new combination, E. deflexa, is proposed for the species.

5. On the basis of a study of the type of *Rollandina capitata* the original description of the species by Patouillard (1905) is emended. This genus is believed to be allied with the Onygenaceae rather than the Gymnoascaceae.

> Rancho Santa Ana Botanic Garden Claremont, California

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