

The genus *Lasiobolus* (Pezizales, Ascomycetes)^{1,2}

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The history of the genus is reviewed and its taxonomical position is discussed. *Lasiobolus* is characterized by small, usually yellowish, setose apothecia, non-septate setae, operculate, non-amyloid, eight-spored to multispored asci, and hyaline to yellowish, smooth, unicelled, thin-walled ascospores that contain gas bubbles. Species are distinguished by (1) the number of spores per ascus, (2) the type and arrangement of excipular cells, (3) presence or absence of cyanophilic markings in the setae, and (4) the relative size and shape of asci, spores, and sterile elements. *Lasiobolus intermedius*, *L. microsporus*, and *L. trichoboloides* are proposed as new species. A key, detailed descriptions, and illustrations are provided for all the 11 recognized species. A list of insufficiently known and excluded species is included.

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Les auteurs considèrent l'histoire du genre et discutent sa position taxonomique. *Lasiobolus* est caractérisé par de petites apothécies généralement jaunâtres, pourvues de soies, par des soies non cloisonnées, par des asques operculés, hyalins, à huit spores ou plus, ainsi que par des ascospores unies, unicellulaires, à paroi mince, contenant des bulles gazeuses. Les espèces se distinguent par (1) le nombre de spores par asque, (2) le type de cellules excipulaires et leur arrangement, (3) la présence ou l'absence de marques cyanophiles dans les soies et (4) la dimension relative et la forme des asques, des spores et des éléments stériles. *Lasiobolus intermedius*, *L. microsporus* et *L. trichoboloides* sont décrits comme nouvelles espèces. Une clef, des descriptions détaillées et des illustrations sont présentées pour les 11 espèces reconnues. L'article comprend une liste d'espèces exclues ou insuffisamment connues.

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Introduction

The genus *Lasiobolus* was proposed by Saccardo (1884) for those species of coprophilous discomycetes with cupulate apothecia, conspicuously setose, with protruding asci and globose to ellipsoidal ascospores. The purpose of Saccardo was to group the setose species of *Ascophanus* Boud. in a separate genus.

Before *Lasiobolus* was established, species later regarded as members of this genus were classified under the genera *Helvella* L. ex St. Amans, *Peziza* Dill. ex Fr., *Ascobolus* Pers. ex Fr., *Humaria* Fckl., *Ascophanus* Boud., and *Lachnea* (Fr.) Gill.

Muller (1778) was the first to deal with a species of *Lasiobolus*, naming it *Helvella equina*.

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His concept of *Helvella* evidently included species with both clavate and cup-shaped apothecia. Muller's species was later placed in *Peziza* by Retzius (1795), Sowerby (1803), Nees von Esenbeck (1817), Gray (1821), Sommerfelt (1826), and Nylander (1869).

Persoon (1794), however, placed all of the cupulate discomycetes known to him in the genus *Peziza*, in which he described his new taxon, *P. papillata*. This was the second specimen of *Lasiobolus* to appear in the literature.

The third species of *Lasiobolus* to be described was placed in the genus *Ascobolus* by Schmidt (1817) as *A. ciliatus*. The genus *Ascobolus* at that time was already well defined according to Durand (1900) and was distinguished from *Peziza* by the protruding tips of the mature asci above the surface of the hymenium.

Persoon (1822) validated both *A. ciliatus* and *P. papillata* but rejected *H. equina* and added a new species, *P. cervina*.

Fries (1822) likewise accepted *A. ciliatus* and *P. papillata* and coined two more names, *Ascobolus pilosus* and *Peziza diversicolor*. All these

names were later transferred to *Lasiobolus*. The name *H. equina* was omitted again.

Wallroth (1833) published *Peziza microscopica*, a species that Rehm (1895) transferred to *Lasiobolus*.

The Crouan brothers (1858) described *Ascobolus pulcherrimus*, which was considered by Schroeter (1893) as a species of *Lasiobolus*.

Karsten in 1861 and 1867, respectively, proposed two new taxa: *Peziza diversicolor* var. *avicularia* and *Ascobolus hirtellus*. These names were later referred to *Lasiobolus* by the same author (1885).

Fuckel described two new species, *Ascobolus albicans* in 1886 and *Ascobolus diversisporus* in 1870, both of which were assigned to *Lasiobolus* by Saccardo in 1889.

When Boudier (1869) erected his genus *Ascophanus*, he placed together several unrelated groups (Kimbrough 1966), but he gave a very lucid treatment to *A. papillatus*, *A. ciliatus*, and *A. pilosus*, which were described separately from the other congeneric species because of their setose apothecia. This work established the basis for the creation of the genus *Lasiobolus* by Saccardo (1884), but unfortunately, Boudier did not treat the following species previously described and mentioned above: *H. equina*, *P. microscopica*, *P. diversicolor* var. *avicularia*, *A. hirtellus*, *A. albicans*, and *A. diversisporus*. *Ascobolus pulcherrimus*, however, was treated among the *Ascobolei excludendi* and was regarded as a *Peziza* species.

Karsten (1870) did not follow Boudier and included the specific epithets "equinus" and "hirtellus" in his section *B* ("sporae incolores"), subsection *b* ("apothecia pilosa") of *Ascobolus*. He described *A. equinus* with two forms, namely, *A. ciliatus* and *A. pilosus*, which were separated from the type on the basis of "differences" in the type of setae. *Peziza papillata*, *P. diversicolor*, and *P. cervina* were considered synonyms of *A. equinus*. *Ascobolus hirtellus* was distinguished from *A. equinus* mainly on the basis of smaller spores, asci, and setae.

Phillips (1878) named a new species of *Ascobolus*, *A. raripilus*, that Saccardo (1889) also combined into *Lasiobolus*. Spegazzini (1878) placed the species *A. diversisporus* and *A. pulcherrimus* in *Humaria* because of the cupulate, setose apothecia of these species. Quelet (1880) described and illustrated *Ascophanus ruber*, another species to be added to *Lasiobolus* by

Saccardo (1889). Gillet (1880) treated *P. papillata*, *P. diversicolor*, and *A. pulcherrimus* in the genus *Lachnea*. Gillet's concept of *Lachnea* was identical with Spegazzini's (1878) definition of *Humaria*.

The establishment of *Lasiobolus* by Saccardo (1884) as a member of the *Ascoboleae* Boud. did not lead to a better understanding of this genus because of his short description and lack of comments. He included *L. papillatus* and *L. pilosus* in the genus, but he did not indicate the type species, gave no synonyms, and did not consider *A. ciliatus* as a member of *Lasiobolus*. Saccardo also did not refer to the species omitted by Boudier (1869) and probably was not aware of those species published after the work of the great French mycologist. The merit of Saccardo's work was that of providing a generic name to apply to those species of *Ascoboleae* with setose apothecia and asci and spores similar to *Ascophanus*.

Later, Saccardo (1889) complemented his earlier work on *Lasiobolus* by giving an improved generic description and listing seven species and two subspecies in the genus.

The following names were added to *Lasiobolus* after its creation in 1884: *L. avicularius* Karsten (1885); *L. hirtellus* Karsten (1885); *L. brachyascus* Marchal (1885); *Lachnea lasioboloides* Marchal (1885); *L. pulcherrimus* (Crouan) Schroeter (1893); *L. horrescens* Rolland (1898); *L. albicans* (Fckl.) Saccardo (1889); *L. dubius* Starback (1904); *L. oligotrichus* A. L. Smith (1916); *L. macrotrichus* Rea (1917); *L. longisetosus* Povah (1929); *L. brachytrichus* Velenovsky (1934); *L. capreoli* Velenovsky (1934); *L. cuniculi* Velenovsky (1934); *L. equinus* var. *major* Velenovsky (1934); *L. leporinus* Velenovsky (1934); *L. minimus* Velenovsky (1939); *L. vaccinus* Velenovsky (1939); *L. aurantiacus* Batista & Maia (1955); *L. pilosus* var. *vaccinus* (Boud.) Gamundi; *L. cainii* Kimbrough & Korf (1967); and *L. monascus* Kimbrough (1974).

Heimerl (1889) rejected the generic rank of *Lasiobolus* and reduced it to a subgenus of *Ascophanus*, in the *Ascobolae*, encompassing only two species, *A. pilosus* and *A. ruber*. He described two forms of *A. pilosus* with spores smaller than 17 microns (μ) and a third one with spore size very close to that of the type. He could not relate his forms of *A. pilosus* with those previously described by Karsten (1870) for *Ascobolus equinus*. Apparently, he did not con-

sider these differences sufficient to separate species. Furthermore, he regarded Karsten's *A. hirtellus* as probably identical with his form 1 of *Ascophanus pilosus* and gave little credit to *A. ruber* as a valid species. Synonyms of his accepted species were not listed.

Rehm (1895) placed *Lasiobolus* together with *Ascophanus*, *Rhyparobius*, *Thelebolus*, and *Zukalina* in the Pseudoascoboleae Boudier. He described *L. equinus* (apparently accepting Karsten's choice of epithet against that of Heimerl), *L. microscopicus*, and *L. pulcherrimus*. According to Rehm, *L. microscopicus* should be removed from the genus. A long list of synonyms was given for *L. equinus*, the name *A. diversisporus* Fckl. was included for the first time in the literature. *Lasiobolus pulcherrimus* was considered by him as related to *Lachnea stercorea*.

Boudier (1907), Migula (1913), and Dennis (1960a) maintained *Lasiobolus* in the tribe Pseudoascoboleae to include the eight-spored, setose species of that group.

Seaver (1928) placed *Lasiobolus* in the tribe Lachneae of the Pezizaceae with two species, *L. equinus* and *L. ruber*. He followed Rehm (1881) in applying the epithet "equinus" and practically accepted all of Rehm's synonyms of *L. equinus*. *Lasiobolus ruber* was given a detailed description and very well separated from *L. equinus*.

Moser (1963) returned *Lasiobolus* to the family Ascobolaceae and presented a key to distinguish between *L. ciliatus* and *L. ruber*.

Kimbrough (1966) kept *Lasiobolus* in the Pseudoascoboleae (= Theleboleae) and cited three common species for North America: *L. equinus* (the type), *L. ruber*, and *L. macrotrichus*. He made a detailed analysis of the structural features of the genus and related it to *Trichobolus*, *Ascophanus*, and *Rhyparobius*. *Lasiobolus* was considered to differ from *Trichobolus* mainly in that the setae are non-septate and the asci are cylindrical with an indented wall at the operculum.

Kimbrough and Korf (1967) emended *Lasiobolus* to include the multispored *L. cainii*. They based their enlargement of the concept of this genus on the notion that the number of spores per ascus was not a valid generic character because of its great instability throughout the tribe Pseudoascoboleae. Theleboleae, a new tribe of Pezizaceae (basonym Thelebolaceae Brefeld), was erected to incorporate *Lasiobolus* and 12 other genera.

Brummelen (1967) proposed the new subfamily Theleboloideae of the Ascobolaceae encompassing *Lasiobolus* and 15 other genera. *Lasiobolus pilosus* was considered to have priority over *L. equinus* based on the erroneous argument that it was an earlier name. *Lasiobolus ciliatus* was not regarded as a synonym of *L. pilosus*. The validity and the generic position of other species belonging or related to *Lasiobolus* were discussed among the insufficiently known and excluded species, such as *L. albicans*, *A. ciliatus* var. *citrinus*, *L. diversisporus*, *L. hirtellus*, *L. microscopicus*, *L. papillatus*, *L. pulcherrimus*, *L. raripilus*, and *L. ruber*.

Eckblad (1968) elevated the Theleboloideae of Brummelen to the rank of family. Practically all genera, including *Lasiobolus*, listed by Kimbrough and Korf (1967) and Brummelen (1967) were maintained in his new family Thelebolaceae. It is worth noting his transfer of *Iodophanus* and *Coprotus* to the Pyronemaceae. Only two species of *Lasiobolus* were treated: *L. pilosus* and *L. ruber*. *Lasiobolus pilosus* was selected as the correct name instead of *L. equinus* because the former species only was used by Fries (1822).

Rifai (1968) accepted the Thelebolaceae of Eckblad (1967) in a scope very similar to the Pezizaceae tribe Theleboleae of Kimbrough and Korf (1967). He described only one species of *Lasiobolus*, which he named *L. ciliatus*. The name *L. pilosus* was added to the synonymy of that species because, according to Rifai, Persoon's revalidation of *A. ciliatus* "has priority over the name *A. pilosus* proposed by Fries." *Ascobolus diversisporus* was not included as a synonym of *L. ciliatus* because an authenticated specimen of that fungus was observed with considerably larger spores.

Kimbrough (1972) referred to the previously described, multispored species *L. cainii* and to an undescribed, uniascal species of *Lasiobolus* (*L. monascus*), which was similar in its superficial appearance to *Trichobolus zukalii* but differed in the nature of the setae and opening of the asci. Thus, *Lasiobolus*, like *Trichobolus* and *Thelebolus*, became a genus consisting of species either with uniascal apothecia and multispored asci or with numerous octosporic asci.

The development of at least two species of *Lasiobolus* has been studied: *L. pilosus* by Borzi (1878); *L. cfr. equinus* by Durand (1970); *L. monascus* by Kimbrough (1974); and *L. ciliatus* by Conway (1974). These authors agree that the

apothecia of *Lasiobolus* have an angiocarpic development (cleistohymenial, opening in the late mesohymenial phase) and that the ascogonial system consists of a septate, multinucleate filament from which one or more cells differentiate and fuse (?) with short branches or protuberances that arise from the same ascogonial filament or the same mother hypha; these cells soon become enveloped by investing hyphae that originate from the basal cells of the ascogonial filament. Croziers were seen by Conway (1974) on the ascogenous hyphae formed by fertile cells of the ascogonium (pleurorhynque type of ascogenous hyphae). The fusion of the fertile ascogonial cells with antheridial cells has not been clearly demonstrated and it might well be that the latter are not functional. Kimbrough (1974) and Conway (1974) pointed out similarities in the ascogonial development of *Lasiobolus*, *Coprobria*, *Cheilymenia*, and *Scutellinia*, and they suggested that *Lasiobolus* could be adequately placed either in the Aleuriaceae sensu Arpin (1968), in Rifai's (1968) Humariaceae, or Korf's (1973) Scutellinoideae of the Pyrenomataceae.

Many of the species pertaining to the genus *Lasiobolus* are poorly described and only a few are well illustrated. *Lasiobolus ciliatus*, *L. lasioboloides*, *L. macrotrichus*, and *L. ruber* are reasonably well understood. Those forms that do not correspond to any of the four species mentioned above are almost impossible to refer to a correct epithet. This situation is quite paradoxical since there seems to be an inflation of specific names in the genus *Lasiobolus*. The purpose of this thesis is, therefore, to provide descriptions, illustrations, and an analytical key to the valid species of *Lasiobolus*, so that, correct identifications can be made.

Materials and Methods

Observations were made mainly on dried specimens, but living material collected in the area of Gainesville was also studied. The fresh material was brought to the laboratory soon after collection and was examined under the stereoscopic microscope to check for the presence of mature fructifications. In many instances, when the apothecia were young or lacking, fragments or pellets of dung were put in petri dishes containing several sheets of wet filter paper. Rose bengal was added sometimes to the water used to wet the petri dishes, in the proportion of 1:30 000, whenever it was necessary to prevent the overgrowth of the substratum by mycelia of fast-growing fungi. Moist chambers were incubated at temperatures between 22 and 26°C in a room where they remained exposed to daylight but not to direct sunlight. After the first appearance of young apothecia

the petri dishes were examined daily until they reached full growth. At this stage, specimens attached to dung fragments were placed in a plant drier for 12 to 24 h. After drying, the material not studied was stored in the herbarium.

Mounting and Staining Procedures

Fresh apothecia were mounted in a drop of water on a slide, placed under the light microscope, and examined for the natural color of the elements. The water was then replaced either by cotton blue in lactic acid as recommended by Le Gal (1947) or by Congo red. The rapid substitution of water by cotton blue in lactic acid prevented the swelling of the structures, and thus accurate measurements could be made. Congo red was used mostly to observe the affinity of the ascus walls, setae, and excipulum to this stain. The reaction of the hymenium and excipulum to iodine was tested with Melzer's reagent as indicated by Dennis (1960a).

Dried specimens were revived either in water or in 5% potassium hydroxide. The latter was used in the case of very old material that would not regain the original shape and size when soaked in water. However, as stated by Brummelen (1967), heating of the dried specimens in lactophenol brought the structures to their approximate original dimensions. Herbarium material was stained in the same way as fresh collections.

Sectioning

Sections of apothecia were made with the cryostat at -20°C. This procedure was useful to observe the structure of the excipulum and implantation of the setae.

Herbarium Material

Collections of dried specimens were obtained from loan from the following herbaria. The abbreviations used are taken from Lanjouw and Stafleu (1964).

- CUP, Department of Plant Pathology, Cornell University, Ithaca, New York, U.S.A.
- FLAS, Mycological Herbarium, University of Florida, Gainesville, Florida, U.S.A.
- LPS, Instituto de Botanica, "C. Spegazzini," La Plata, Argentina.
- NY, The herbarium of the New York Botanical Garden, New York, U.S.A.
- PC, Museum National d'Histoire Naturelle, Laboratoire de Cryptogamie, Paris, France.
- PR, Botanické oddelení Národního muzea, Praha, Czechoslovakia.
- TRTC, Cryptogamic Herbarium, University of Toronto, Toronto, Canada.
- UC, Herbarium of the University of California, Department of Botany, Berkeley, U.S.A.
- URM, Instituto de Micologia, Universidade Federal de Pernambuco, Recife, Brasil.

Observations

Substrate

All known species of *Lasiobolus* are coprophilous. Herbivores' dung is the most common substratum for most species, but they also occur on dung of carnivores and omnivores. Karsten (1870) reported one collection of *Lasiobolus equinus* from human feces. *Lasiobolus aurantiacus*

and *L. horrescens* were collected on substrates other than animal dung; however, both species have to be transferred to other genera because of discrepancies in ascospore and setae characters. With the exception of *Lasiobolus monascus*, known only from its original collection on rabbit dung, all members of *Lasiobolus* have been found on dung of various animals. Specialization towards a particular substrate has not been demonstrated in any species.

Distribution

Since *Lasiobolus* species have not been extensively collected, especially in tropical regions, it is difficult to draw valid conclusions about their distribution. Most collections available today originate from localities in Europe, the United States, and Canada. Few specimens have been examined from Central and South America, Asia, Africa, and Australia. Despite the present lack of information, it is possible to point out those species that are cosmopolitan and those that seem to be restricted to the temperate regions of the globe. No species was found to be exclusively tropical. *Lasiobolus cainii*, *L. ruber*, and *L. lasioboloides* are perhaps confined to cold climatic regions. The first species has not yet been found outside Canada. *Lasiobolus lasioboloides* has been collected in Europe, the United States, and Canada, while *L. ruber* is found in temperate areas of both hemispheres.

Lasiobolus intermedius and *L. macrotrichus* would have the same pattern of distribution as *L. lasioboloides* were it not for recent collections of these species made in New Zealand. *Lasiobolus ciliatus*, *L. cuniculi*, *L. diversisporus*, *L. oligotrichus*, and *L. trichoboloides* are included among the cosmopolitan species. *Lasiobolus ciliatus* is the most common species of all. *Lasiobolus microsporus* has been collected several times in Canada and once in the West Indies. This species may have a wide range of distribution.

Biology and Development

The biology of the species of *Lasiobolus* is identical with the coprophilous members of the Ascobolaceae and Thelebolaceae as reviewed by Brummelen (1967) and Conway (1974), respectively. These organisms have in common such features as a life cycle that includes the passage of the ascospores through the intestinal tract of animals, the forcible ejection of the ascospores, and the positive phototropic response of the asci. As in *Ascobolus* (Brummelen

1967) many asci in the same apothecia discharge their spores simultaneously.

The ascocarps show homothallic development from single spores after they have passed through the digestive tract of grazing animals. Under laboratory conditions, 2% KOH will induce spore germination on a number of media. During the ontogeny of the ascocarps, the ascogenous system is enclosed very early by the developing archicarp, which becomes setose as it increases in size and finally opens in the late mesohymenial phase (Conway 1974).

Mycelium

The mycelium of *Lasiobolus* develops within the substrate and becomes restricted at maturity to an inconspicuous "rooting" system at the base of the apothecium. In nature, the hyphae that radiate from the basal part of the excipulum attaching the apothecia to the substratum are hyaline to yellowish, generally non-septate, and unbranched. In culture, however, the hyphae are septate, branched, and with uninucleate cells (Conway 1974).

Apothecia

The apothecia are easily seen in good specimens because of their usually bright color, setose nature, and dense population on the colonized substrates. Dried specimens with few, pallid ascocarps need to be carefully examined under the dissecting microscope or the fungus may be overlooked. The apothecia are superficial, sessile, with an exposed hymenium at maturity; they are at first globose, but later their shape varies from obconical, obpyriform, or turbinate to shallow funnel-shaped or cupulate (Figs. 9D, 12). The intensity of their color depends on the exposure to light and perhaps on the kind of substrate. Apothecia that developed in crevices of the substrate display a lighter coloration than those exposed to direct light. The same species often show apothecia of different color intensities when collected in distinct substrates; however, it is not known whether this reflects a nutritional effect or not.

The anatomy of an apothecium consists of a *disc* or *hymenium* (fertile part) and a *receptacle* (supporting structure). The receptacle in section is composed of an outer wall, the *ectal excipulum*, and inner layers of tissue, the *medullary excipulum* or flesh. The *subhymenium* or *hypothecium*, a thin hyphal layer beneath the hymenium, is usually inconspicuous. Stiff appendages,

the *setae*, arise from the peripheral layer of the excipulum conferring a hairy appearance to the apothecia.

Excipulum

The ectal excipulum is generally thicker towards the base than near the margins, which are entire. The ectal cells are cyanophilous, dextrinoid, and vary in size and shape from the marginal to the basal regions. Near the margins they are elongated, angular, or lobed and are arranged horizontally with their long axis parallel to the surface of the hymenium, forming a *textura epidermoidea* type of tissue (Figs. 20, 21, 22, 23). This is the case of most species, such as *Lasiobolus ciliatus*, *L. ruber*, and *L. microsporus*. In *Lasiobolus cainii* and *L. trichoboloides* the ectal cells are arranged vertically with their long axis perpendicular to the surface of the hymenium, giving an impression of a *textura prismatica* tissue (Figs. 1E, 11D). The ectal cells near the base become larger, angular, and almost isodiametric (*textura angularis*) in all species.

The ental or medullary excipulum is formed by longer cells and hyphal elements, especially towards the subhymenium, giving rise to a *textura angularis* or *intricata* tissue.

Setae

The *setae* originate superficially from the outer layer of ectal cells at the base and sides of the apothecia. None of the specimens studied showed *setae* arising from the edge of the margins of the excipulum despite Boudier's (1869) reference to setose margins in *Lasiobolus ciliatus*. They are bristly, straight, hyaline to light yellowish, acute, and usually non-septate (Figs. 18, 19). *Lasiobolus monascus* and *L. trichoboloides* differ from other species in that they have both non-septate and one to two septate *setae* (Fig. 9C). The shape of the *setae* varies from typically ventricose, barrel-shaped at the base in *Lasiobolus ciliatus* to almost cylindrical-acicular in *L. lasioboloides* and *L. trichoboloides* (Figs. 6D, 11D). The walls are thick, transparent, smooth or incrustated with cyanophilous granules. Congo red usually strongly stains the walls and cytoplasm of the *setae*.

Asci

Asci are cylindrical to clavate cylindrical, short-stalked, operculate, non-amyloid, and protruding above the surface of the hymenium at spore liberation (Figs. 24, 25). The number of ascospores per ascus is eight in all species,

with the exception of *Lasiobolus cainii*, which has 80–100 ascospores per ascus, and *L. monascus*, which has more than 500 spores per ascus. The hymenium is polyascal in all species but in the uniascal *Lasiobolus monascus*. The ascus wall is constructed of two inseparable layers, the outer one is indented at the point of the operculum and stains uniformly around the base and apex in Congo red (Kimbrough 1966). The operculum is formed at the last phase of maturation through an indistinct line of dehiscence in the ascus wall and remains attached at one side after releasing the spores.

Ascospores

The ascospores are unicellular and quite variable in size, ranging from 7.5 to 34.5 μ long and 4.5 to 19.5 μ broad. Their shape is fairly constant within each species, but it varies from subglobular or ellipsoidal to oblong or almost fusiform among different species (Figs. 26, 27). The spore wall is quite thick at first but becomes relatively thin by the time of spore liberation. A delicate, smooth sheath similar to that described by Le Gal (1947) in *Cheilymenia theleboloides* (Alb. & Schw. ex Pers.) Boud. often becomes visible when the spores are heated in lactic acid–cotton blue. Most species have hyaline spores, but they can become yellowish-brown especially in *Lasiobolus diversisporus*. Spore protoplasm is devoid of visible oil guttules and has a single nucleus and a prominent deBary bubble (Fig. 27). The arrangement of the spores within the ascus is uniseriate to irregularly biseriate, with the exception of the multispored *Lasiobolus cainii* and *L. monascus*, which are densely clustered (Fig. 1D).

Paraphyses

The paraphyses are hyaline, filiform, septate, branched, and anastomosed in some species, with slightly or strongly swollen tips (Figs. 28, 29). The cytoplasm is granular, with oil guttules, and, in specimens submitted to intense light, rich in carotenoid pigments, which give a yellow or orange color to the hymenium (Fig. 30). According to Berthet (1964) each cell is uninucleate but sometimes binucleate.

Family Relationship

Both *Lasiobolus* and *Thelebolus* include forms with either eight-spored or multispored asci that protrude beyond the hymenial level. Eckblad (1968) regards the protruding nature of the asci

as of high taxonomic value. Kimbrough *et al.* (1969), however, dealing with the genus *Iodophanus*, noted that "while protruding asci are evident in coprophilous species, they are less evident or nonexistent in the lignicolous and terrestrial forms" and concluded that "protruding asci might be an ecological adaptation." Since Conway (1974) found important differences in the development and ascus structures of *Lasiobolus* and *Thelebolus*, we tend to agree that the similarities between both genera are superficial and represent convergent adaptation to the coprophilous habitat. In synthesis, Conway (1974) observed that *Thelebolus stercorarius* opens in the telohymenial phase, does not form croziers, and does not have an operculum; while *Lasiobolus ciliatus* opens in the late mesohymenial phase, forms croziers, and is operculate. These differences suggest that *Lasiobolus* should be removed from the Thelebolaceae.

The development of a stalked ascogonium, which is soon enveloped by hyphae originated from the stalk as described by Kimbrough (1974) and Conway (1974) for *Lasiobolus* species, was also reported for *Coprobria granulata* (Blackman and Fraser 1906; Gwynne-Vaughan and Williamson 1930), for *Cheilymenia stercorea* (Fraser 1907), and for *Scutellinia scutellata* (Brown 1911). These species also share some morphological and microchemical features with *Lasiobolus*, such as apothecia setose, ectal excipulum dextrinoid and cyanophilic, and ascospores with a delicate outer wall usually separable when heated in lactic acid.

Based on these developmental, morphological, and microchemical similarities it appears that *Lasiobolus* is more related to *Cheilymenia*, *Coprobria*, and *Scutellinia* than to *Thelebolus*.

Cheilymenia, *Coprobria*, and *Scutellinia* were placed by Rifai (1968) in the tribe Ciliarieae of the Humariaceae. This tribe included the genera of Humariaceae with usually setose apothecia, carotenoid pigmentation, disc yellow to orange, and ascospores ornamented or smooth but with their outer walls readily becoming loose when heated in lactic acid.

Eckblad (1968) treated the Humariaceae as a synonym of Pyrenomaceae where he accommodated the 3 genera cited above together with 18 other genera. This family was taken in a wide sense and consists of forms with apothecia glabrous or setose, disc brightly colored, whitish or brown, asci non-amyloid or sometimes amyloid, ascospores globose to fusoid, smooth or

with a callose-pectic type of ornamentation, and paraphyses mostly containing carotenoid granules.

Dennis (1968) considered *Scutellinia* and *Cheilymenia* in the tribe Ciliarieae of the Humariaceae. However, *Coprobria* was placed in the tribe Aleuriaceae of the same family because of the absence of true setae in the apothecia. His concept of the Humariaceae was almost as broad as Rifai's (1968); however, he did not consider the tribe Otideae to belong in this family. The Humariaceae was briefly defined as having usually setose apothecia, hymenium mostly brightly colored, asci non-amyloid, and paraphysis with carotenoid pigments.

Arpin (1968) defined his family Aleuriaceae as consisting of genera with apothecia glabrous or setose, disc yellow to brown, asci non-amyloid, ascospores smooth or with callose-pectic ornaments, and paraphyses with carotenoid pigments. *Coprobria*, *Cheilymenia*, and *Scutellinia* were placed in the group *a* of the Aleuriaceae.

Kimbrough (1970) accepted the Aleuriaceae of Arpin and suggested the addition of *Fimaria*, *Leucoscypha*, *Lamprospora*, *Inermisia*, *Genosperma*, and *Rhizoblepharis* to the family.

Korf (1973) divided the Pyrenomataceae in five subfamilies: Ascodesmidoideae, Pyronematoideae, Ascosphanoideae, Otideoideae, and Scutellinioideae. The genus *Lasiobolus* was assigned to the Ascophanoideae and *Scutellinia*, *Cheilymenia*, and *Coprobria* were included in the Scutellinioideae. These two subfamilies were distinguished on basis of the presence or absence of deBary bubbles and carotenoid pigments.

Contrary to Rifai (1968), who considered *Cheilymenia* and *Lasiobolus* as unrelated because, according to him, their "ascospores characters, the anatomy of their apothecia and the structures of their hairs are markedly different," Kimbrough (1974) and Conway (1974) recognized morphological and ontogenetical similarities between *Lasiobolus*, *Coprobria*, *Scutellinia*, and *Cheilymenia* and advocated the inclusion of *Lasiobolus* in the family Aleuriaceae or in the tribe Ciliarieae. Conway (1974) was unaware of the existence of carotenoids in *Lasiobolus*, but he did not consider this character as a serious obstacle to the inclusion of *Lasiobolus* in the Aleuriaceae. Our observations on the presence of an outer separable sheath in the ascospores and carotenoids in the paraphyses of *Lasiobolus* seem to add more credence to the views of Kimbrough and Conway.

If one regards the deBary bubbles in the ascospores, the non-septation, and the superficial implantation of the setae of *Lasiobolus* species as insufficient characters to distinguish between families, subfamilies, or tribes as implied by Kimbrough and Conway, the best solution is to place this genus together with *Cheilymenia*, *Coprobia*, and *Scutellinia* in the same group, such as the tribe Scutellinieae of Korf (1973).

Although *Lasiobolus* could belong in the tribe Scutellinieae, we feel that the family position is still an open question since the Pyrenomataceae sensu Korf (1973) or sensu Eckblad (1968) incorporates such a wide variety of developmental, morphological, and microchemical forms. We feel that the Pyrenomataceae should be restricted to those genera that have clusters of ascogonia and gymnocarpic development, such as *Pyronema* and *Coprotus*.

Taxonomy of *Lasiobolus*

Lasiobolus Saccardo, in Bot. Centr. Bl. 18: 220. 1884.

TYPE SPECIES (selected): *Ascobolus pilosus* Fr. = *Lasiobolus ciliatus* (Schmidt ex Pers.) Boud.

Apothecia small, gregarious to densely crowded, sessile. Disc flat or convex, roughened by protruding asci, yellowish or reddish orange, red or whitish. Receptacle from obconical or turbinate to funnel-shaped, cupulate or pulvinate, setose. Setae superficial, thick-walled, pointed, from acicular to ventricose at the base, non-septate or rarely septate near the base, hyaline, short or long. Ectal excipulum dextrinoid, cyanophilic, thin around the hymenium and thick towards the base, of angular, lobed, or quadratic cells (usually textura epidermoidea, rarely prismatica or angularis). Medullary excipulum of delicate, hyaline cells, of textura intricata or angularis. Hymenium multiascal or uniascal. Asci cylindrical to broadly clavate, rarely pyriform, pedicelate, eight- to many-spored, non-amyloid, operculate. Ascospores uniseriate to conglobate, smooth-walled, hyaline to yellowish, without apparent oil droplets, with deBary bubbles, narrow or broad ellipsoidal, with a delicate outer sheath that sometimes peels off and becomes visible in heated cotton blue in lactic acid. Paraphyses filiform, septate, simple or branched, apex straight, usually inflated, containing pigmented granules.

HABITAT: On various kinds of dung.

KEY TO THE SPECIES OF LASIOBOLUS

- A. Asci eight-spored C
- A. Asci containing more than eight spores B
- B. Apothecia multiascal *L. cainii* (1)
- B. Apothecia uniascal *L. monascus* (9)
- C. Ascospores longer than 20 μ G
- C. Ascospores shorter than 20 μ D
- D. Setae cylindrical acicular E
- D. Setae subventricose at the base F
- E. Ascospores 13–18 × 9–13.5 μ, ectal cells horizontally oriented *L. lasioboloides* (6)
- E. Ascospores 8.5–11.5 × 6–9 μ, ectal cells vertically oriented *L. trichoboloides* (11)
- F. Ascospores 13–18 × 7.5–11.5 μ, setae usually smooth *L. intermedius* (5)
- F. Ascospores 9–11 × 6.6–8.0 μ, setae always with cyanophilic markings *L. microspor* (8)
- G. Setae 600 μ long or more H
- G. Setae less than 600 μ long I
- H. Ascospores 15–23 × 6–13 μ, narrow ellipsoidal, asci cylindrical *L. macrotrichus* (7)
- H. Ascospores 22–30 × 9–13.5 μ, subfusiform, asci clavate *L. ruber* (10)
- I. Ascospores 24–34 × 12–19 μ, becoming yellowish when mature *L. diversisporus* (4)
- I. Ascospores smaller, 18–24 × 12–14 μ, remaining hyaline H
- H. Asci broadly clavate, setae subventricose, up to 24 μ diam at the base *L. cuniculi* (3)
- H. Asci cylindrical or clavate cylindrical, setae ventricose, up to 42 μ at the base *L. ciliatus* (2)

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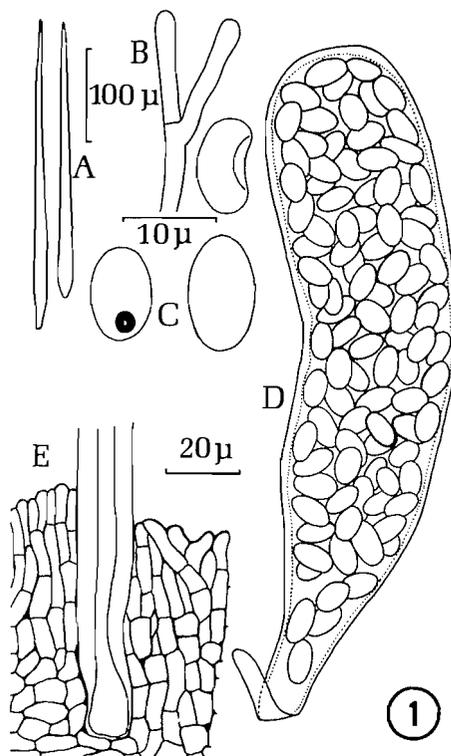


FIG. 1. *Lasiobolus cainii*. A. Setae. B. Branched paraphysis. C. Ascospores, one with a deBary bubble. D. Ascus and ascospores. E. Ectal cells and attachment of a seta.

(1) *Lasiobolus cainii* Kimbrough, Am. J. Bot. 54 (1): 20. 1967. Figs. 1, 28

Apothecia scattered to gregarious, sessile, 400–800 μ diam. Disc flat, without margins, yellowish to orange. Receptacle cupulate, concolorous with the disc, setose. Setae arising from the lower and median parts of the receptacle, non-septate, bristly, acute, 180–500 μ long by 6–20 μ diam at the slightly bulbous base; walls smooth, 3–4.5 μ thick. Ectal excipulum of elongate or quadratic, vertically oriented cells, 5–24 \times 4–8 μ , textura angularis to epidermoidea. Medullary excipulum of thin, hyaline cells, textura intricata. Subhymenium inconspicuous. Hymenium multiascal, I(–). Asci broadly clavate, truncate above, attenuate below, stalked, 210–240 \times 42–48 μ , staining uniformly in Congo red, 80- to 100-spored. Ascospores conglobate, hyaline, ellipsoidal, rounded at both ends, often collapsed at one side, smooth-walled, 10.5–15.0 \times 6.0–8.5 μ , each with a prominent deBary bubble. Paraphyses filiform, numerous, septate, extending beyond the asci, 2.5–3.0 μ diam.

HABITAT: On dung of porcupine and rabbit.

NAME: After Dr. Roy F. Cain

SPECIMENS EXAMINED: CANADA: *Cain* 6693, Gomphidius Bay, Lake Timagami, Ontario, 3.VIII.1936 (TRTC-46531, 46532); *Cain* 11055, Bear Island, Lake Timagami, Ontario, 15.VIII.1938 (TRTC-46530, CUP-47671); *Cain*, Bear Island, Lake Timagami, Ontario, 7.IX.1935 (TRTC-40007); *Cain*, Diamond Lake, Timagami, 2.IX.1935 (TRTC-40008, CUP-47606); *Cain* 36087, Atkins Lake, Muskoka, Ontario, 2.IX.1932 (TRTC).

(2) *Lasiobolus ciliatus* (Schmidt ex Pers.) Boud., Hist. Class. Discom. Eur. 78. 1907.

Figs. 2, 13, 18, 22, 30
 \equiv *Ascobolus ciliatus* Schmidt in Mycol., Hefte 1, p. 90. 1817.

\equiv *Ascobolus ciliatus* Schmidt ex Pers., Mycol. eur. 1: 340. 1822.

\equiv *Ascophanus ciliatus* (Schmidt ex Pers.) Boud. in Ann. Sci. Nat. (Bot.) V, 10: 354. 1869.

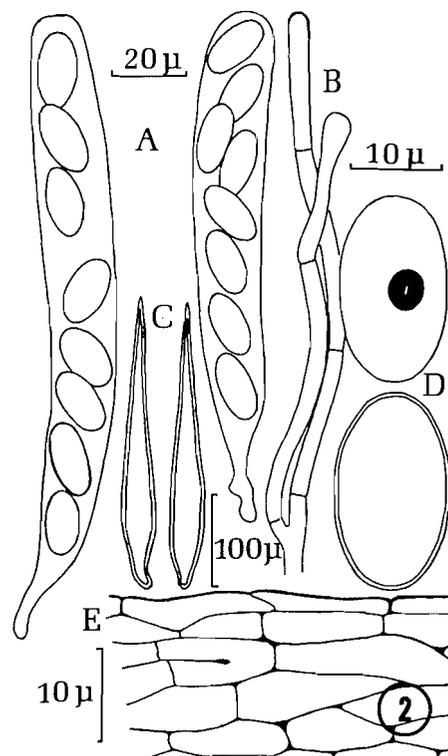


FIG. 2. *Lasiobolus ciliatus*. A. Asci and ascospores. B. Branched paraphysis. C. Setae. D. Ascospores, one with a deBary bubble. E. Ectal cells.

- = *Peziza equina* (Mull.) ex S. F. Gray var. *ciliata* (Schmidt ex Pers.) Karst., Mycol. Fenn. 1: 73. 1871.
 = *Ascophanus pilosus* (Fr.) Boud. var. *ciliatus* (Schmidt ex Pers.) Phill., Man. Br. Discom. 312. 1887.
 = *Lasiobolus equinus* (Mull. ex S. F. Gray) Karst. subsp. **Lasiobolus ciliatus* (Schmidt ex Pers.) Sacc., Syll. Fung. 8: 537. 1889 (ut "**L. Ciliatus* (Berk.) Sacc.>").
 = *Elvella equina* Mull. in Fl. dan. 5(13): 8. 1778.
 = *Peziza equina* (Mull.) ex S. F. Gray, Nat. Arrang. Br. Plants, 1: 666. 1821.
 = *Ascobolus equinus* (Mull. ex S. F. Gray) Karst. in Not. Sallsk. Fauna Fl. Fenn. 11: 209. 1870.
 = *Lasiobolus equinus* (Mull. ex S. F. Gray) Karst. in Acta Soc. Fauna Fl. Fenn. 2: 122. 1885.
 = ?*Peziza papillata* Pers. in Neues Mag. Bot. 1: 115. 1794.
 = *Peziza papillata* Pers. ex Fr., Syst. Mycol. 2: 88. 1822.
 = *Ascobolus papillatus* (Pers. ex Fr.) Wallr., Fl. crypt. Germ. 2: 514. 1833.
 = *Ascophanus papillatus* (Pers. ex Fr.) Boud. in Ann. Sci. Nat. (Bot.) V, 10: 252. 1869 (misapplied?).
 = *Lasiobolus papillatus* (Pers. ex Fr.) Sacc. in Bot. Club, 18: 220. 1884.
 = *Ascobolus pilosus* Fr., Syst. Mycol. 2: 164. 1822.
 = *Ascophanus pilosus* (Fr.) Boud. in Ann. Sci. Nat. (Bot.) V, 10: 254. 1869.
 = *Ascobolus equinus* (Mull. ex S. F. Gray) Karst. subsp. **Ascobolus pilosus* (Fr.) Karst. in Not. Sallsk. Fauna Fl. Fenn. 11: 210. 1870.
 = *Peziza equina* (Mull.) ex S. F. Gray var. *pilosa* (Fr.) Karst., Mycol. Fenn. 1: 73. 1871.
 = *Lasiobolus pilosus* (Fr.) Sacc. in Bot. Club, 18: 220. 1884.
 = *Lasiobolus equinus* (Mull. ex S. F. Gray) Karst. subsp. **Lasiobolus pilosus* (Fr.) Sacc., Syll. Fung. 8: 537. 1889.
 = *Peziza cervina* Pers., Mycol. eur. 1: 254. 1822.
 = *Peziza diversicolor* Fr., Syst. Mycol. 2: 88. 1822.
 = *Lachnea diversicolor* (Fr.) Gill., Champ. Fr., Discom. 81. 1880.
 = *Scutellinia diversicolor* (Fr.) Lamb., Fl. mycol. Belg., Suppl. 1: 301, 1887.
 = *Peziza stercorea* (Wigg.) ex S. F. Gray var. *equina* Pers., Mycol. eur. 1: 247. 1822 (sensu Boudier 1869).
 = *Ascophanus pilosus* (Fr.) Boud. var. *equinus* (Pers.) Boud. in Ann. Sci. Nat. (Bot.) V, 10: 255. 1869.
 = *Ascophanus pilosus* (Fr.) Boud. f. *equinus* (Pers.) Rehm in Ber. Nat. Ver. Augsburg, 26: 28. 1881 (ut f. *equinus* Boud.).
 = *Ascophanus pilosus* (Fr.) Boud. var. *vaccinus* Boud. in Ann. Sci. Nat. (Bot.) V, 10: 255. 1869.
 = *Ascophanus pilosus* (Fr.) Boud. f. *vaccinus* (Boud.) Rehm in Ber. Nat. Ver. Augsburg, 26: 28. 1881.
 = *Lasiobolus pilosus* (Fr.) Sacc. var. *vaccinus* (Boud.) Gamundi in Darwiniana, 13: 602. 1964.
 Apothecia gregarious, sessile, 300–750(–900) μ diam. Disc flat or convex, rough, from light yellowish to orange. Receptacle at first globose, then turbinate, and finally cupulate or shallow funnel-shaped, of the same color or paler than the disc, setose; anchoring hyphae subhyaline or yellowish, non-septate, unbranched, 2–5 μ diam. Setae arising from the lower and median part of the receptacle, non-septate, stiff, pointed, distinctly ventricose at their bases, 200–600 μ long by (12–)20–42 μ diam, at the widest part; walls smooth, Congo red positive, 3–6 μ thick. Ectal excipulum 10–17 μ thick around the hymenium, of angular, lobed, elongated, 5–24 \times 2–9 μ , horizontally oriented cells, a textura epidermoidea; the ectal excipulum becomes thicker, 30–50 μ thick, towards the base of the receptacle, of angular, isodiametric cells, 10–20 μ diam, a textura angularis. Medullary excipulum of narrower, hyaline, cells. Subhymenium inconspicuous. Hymenium multiascal about 200 μ thick, I(–). Asci clavate cylindrical, rounded or truncate above, attenuated below into a stalk, (112–)180–270 \times 15–30 μ , eight-spored. Ascospores uniseriate or biseriate, hyaline, ellipsoidal, rounded at both ends, smooth-walled, (17–)19–25 \times (9–)12–14(–15) μ , each with a prominent deBary bubble. Paraphyses hyaline, filiform, septate, branched, 2–2.5 μ diam below, slightly inflated to 2.5–3.5 μ at their apices.
 HABITAT: On various kinds of dung, including human feces (Karsten 1870).
 NAME: Referring to the setose apothecia.
 SPECIMENS EXAMINED (in parenthesis is the number of specimens examined for each country or American state; only a few of these are cited):

UNITED STATES: Florida (9): *Kimbrough*, Millhopper Rd., 8 mi NW of Gainesville, 19.IV.1970 (FLAS-F48950); *Kish*, Sugarfoot Hammock, SW 20th Ave., Gainesville, 28.I.1971 (FLAS-F49065); *K. & C. Conway*, San Felasco Hammock, 12 mi NW of Gainesville, 31.III.1969 (FLAS-F48533); Georgia (1): *Massee*, Princeton, 21.II.1931 (NY); Alabama (1): *Earle & Underwood A-1239*, Auburn, Lee Co., 11.VI.1896 (NY); New York (5): *Durand* 866, Cornell University Farm, Cayuga Lake Basin, 17.IV.1895 (TRTC); *Clinton*, Buffalo, s.dat. (NY); *Luck-Allen*, Winnie Hill, Otsego Co., 21.IX.1963 (TRTC); New Jersey (1): *Ellis*, Newfields, 2.VII.1855 (NY); Massachusetts (3): *Clarke* 2334, Jamacica Plain, III.1889 (NY); *Sturgis*, Cambridge, XII.1890 (NY); Ohio (1): *Morgan* 26, Preston, II.1891 (NY); Indiana (1): *Muller* 6715, Goshen, 1.XI.1934 (TRTC-46527); Iowa (4): *Martin* 3877, Iowa City, 24.IV.1937 (TRTC); *Seaver* 48b, Iowa City, 2.V.1904 (NY); Kansas (1): *Kellerman*, Manhattan, VI.1885 (NY); North Dakota (1): *Cain*, Medora, Billings Co., 5.IX.1957 (TRTC); Wyoming (5): *Solheim* 3739, Grand Teton Natl. Pk., 29.VI.1955 (UC-205778); *Cain* 43422, Yellowstone Pk., Lower Geyser Basin, 1.IX.1962 (TRTC); *Cain* 43811, Boller, Albany Co., 1.IX.1964 (TRTC); Montana (5): *Cain* 42205, Treasure Co., Big Horn, 4.IX.1957 (TRTC); *Cummins* 74, Bigfork, 20.VIII.1929 (NY); *Cain* 42222, Yellowstone Pk., Lower Geyser Basin, 1.IX.1962 (TRTC); Idaho (1): *Cain*, Fremont Co., 1.IX.1962 (TRTC); California (2): *Setchell*, Greenville Woods, Norwich, 10.IX.1888 (UC-48580); *Parks*, s. loc., s. dat. (UC-513715); Oregon (2): *Luck-Allen*, Stinking Water Mts., Harney Co., 30.VIII.1962 (TRTC). CANADA (33): *Cain* 3724, Black River, Thunder Bay, Ontario, 21.VI.1963 (TRTC); *Krug*, La Cloche Mts., NE of Kittarney, Ontario, 26.V.1962 (TRTC); *Heimbürger*, Lake Kluane, Silver City, Yukon, 18.VII.1963; *Luck-Allen*, Alta, Wapeti Prov., Jasper, 8.VIII.1962 (TRTC-40169); *Rousseau* 32010, George River, Racicot Rapids, Ungawa, Quebec, 17.VII.1947 (TRTC); *Soper* 39298, Ellesmere Island, Lake Hazen, summer 1958 (TRTC); *Soppit*, Halifax, 5.IX.1892 (CUP-216). MEXICO (1): *Lemke*, roadside hwy. 140, 25.V.1962 (TRTC). BERMUDA (10): *Seaver & Waterson* 353, Paget Marsh, 28.IX.1940 (NY). VENEZUELA (4): *Dumont et al.*, Laguna Mucubaji, Parque Nacional Sierra Nevada, near Apartaderos, Merida, 17.VII.1971 (FLAS-F49569); *Dumont*

et al., La Agua, El Teleferico above Merida, 17.VII.1971 (FLAS-F49571). BRAZIL (2): *Rick* 6645, São Leopoldo, Rio Grande do Sul, 1904 (TRTC); *Rick* 48, São Leopoldo, 1904 (PC). PARAGUAY (1): *Spegazzini* 6857, Asuncion, X.1919 (TRTC). ARGENTINA (1): *Spegazzini* 6836, La Plata, 23.VIII.1888 (TRTC). GERMANY (7): *Auerswald*, Leipzig, 9.X.1863 (NY); *Feurich*, Rachtal, 17.VI.1900 (PR-728144); *H. & P. Sydow* 1642, Branderburg, Nieder-Barnim, 30.III.1918 (PR-728136, 728140); *Drieger* 2214, Königstein, Saxonien, IV.1883 (NY). BELGIUM (1): *Marchal* 3068, Brussel, III.1884 (NY). ENGLAND (3): *Wheldon* 1365, S. of Lancashire, VIII.1912 (NY). CZECHOSLOVAKIA (14): *Kotlaba*, Blata pr. Sobeslav, 20.IX.1953 (PR-728132); *Kubicka*, Sumava Mts., 31.V.1953 (PR-728127); *Moravec*, Nizke Tatry Mts., Chopok Mt., 7.IX.1960 (PR-614230); *Svrcek*, Uvaly pr. Praga, IV.1967 (PR-728124); *Vacek*, Iv. Jan pod skalom, 17.V.1942 (PR-728135); *Velenovsky*, Radohn, VI.1927 (PR-151713, associated with *Lasiobolus cuniculi*); *Vichandsky*, Dolni Jircany pr. Jilove, 2.V.1953 (PR-728134). AUSTRIA (1): *Fuckel* 1302, Nassau, Austria, s. dat. (TRTC). SWITZERLAND (1): *Cain*, Graubunden, Wiesen, 28.VIII.1971 (TRTC-46389). FRANCE (2): *Ludwig*, Bois du Meudon, VIII.1907 (PC); *Le Breton* 5925, Rouen, France, s. dat. (NY). ITALY (1): *Cavara* 222, "circa Papiam," s. dat. (NY). SWEDEN (1): *Nannfeldt* 9675, Bondkyrka parish, Svin-skinnsskogen, 14.XI.1947 (NY).

(3) *Lasiobolus cuniculi* Vel., Monogr. Discom. Bohem. 1: 413. 1934. Figs. 3, 21, 25 = *Lasiobolus leporinus* Vel., Monogr. Discom. Bohem. 1: 413. 1934. = *Lasiobolus brachytrichus* Vel., Monogr. Discom. Bohem. 1: 362-363. 1934.

Apothecia gregarious, sessile, 200-700 μ diam, 250-400 μ high. Disc flat, yellowish, without margins. Receptacle obconical to cupulate, setose, concolorous with the disc; anchoring hyphae flexuous, non-septate, sparingly branched, subhyaline, 2.5-4.0 μ diam. Setae arising superficially from the lower and median parts of the receptacle, stiff, straight, pointed, subventricose at their bases, 100-450 μ long by 10-24 μ diam at the widest part. Ectal excipulum 9-11 μ thick around the hymenium composed of three or four layers of small, elongated, lobed, horizontally oriented cells, 7-15 \times 3-8 μ , a textura epidermoidea. Medullary excipulum of hyaline, thin-walled, narrow cells. Subhymenium in-

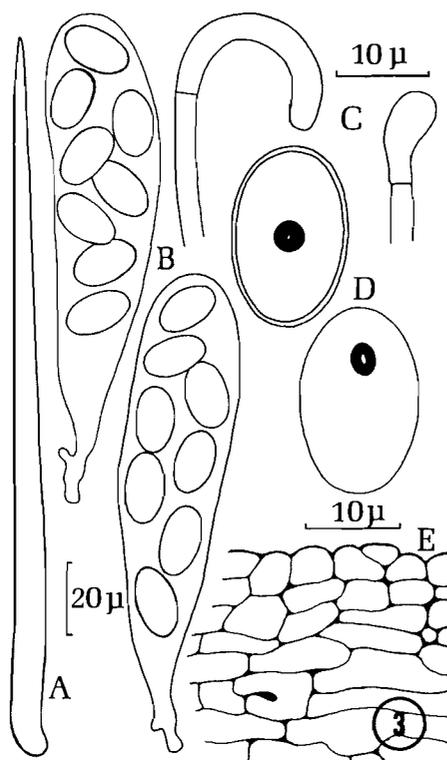


FIG. 3. *Lasiobolus cuniculi*. A. Seta. B. Asci and ascospores. C. Paraphyses apices. D. Ascospores with deBary bubbles. E. Ectal cells.

conspicuous. Hymenium multiascal, 200–220 μ thick, I (–). Asci broadly clavate, rounded above, abruptly constricted below, short pedicelate, 100–215 \times 19–36 μ , eight-spored. Ascospores biserial or obliquely uniserial, hyaline to subhyaline, ellipsoidal, rounded at both ends, smooth-walled, (16–) 18–24(–26) \times (9–)12–14(–16) μ , each with a conspicuous deBary bubble. Paraphyses hyaline, filiform, septate, simple or branched, slightly inflated to 3.0–4.5 μ diam at their apices.

HABITAT: On dung of rabbit, hare, sheep, goat, racoon, cow, horse, and other animals.

NAME: Referring to the original collection on rabbit dung.

SPECIMENS EXAMINED (atypical specimens with question marks): UNITED STATES: *Bezerra*, Austin Cary Forest, Alachua Co., Florida, 5.VIII.1973 (FLAS-F50274); *Commons 2009*, Wilmington, Delaware Co., New York, 8.X.1892 (NY); *Seaver*, Portland, Connecticut, 3.IX.1914 (NY); *Bethel 2*, Caribou, Colorado, 19.VII.1929 (NY); *Seaver & Shope 98*, Univ. of Colorado Campus, Colorado, 29.VII.1929 (NY); *Cain 41603*, Roosevelt Natl. Forest, Larimer Co., Colorado,

17.VIII.1957 (TRTC); *Cain*, Roosevelt Natl. Forest, Larimer Co., Colorado, 17.VIII.1957 (TRTC-46639); ?*Cain*, Larimer Co., Colorado, 19.VIII.1957 (TRTC-46644); *Cain 39132*, Sundance, Crook Co., Wyoming, 3.IX.1962 (TRTC); *Cain 3235 a + b*, Moran, Teton Co., Wyoming, 3.VII.1964 (TRTC); *Cain 43404*, Bosler, Albany Co., Wyoming, 1.IX.1964 (TRTC); *Cain 43392*, Bosler, Albany Co., Wyoming, 1.IX.1964 (TRTC); *unknown collector*, Mariposa Co., California, 24.VII.1966 (TRTC-46647); ?*Luck-Allen 40425*, S of Sisters, Deschutes Co., Oregon, 30.VIII.1969 (TRTC); ?*Cain 39879*, Targhee pass, Fremont Co., Idaho, 1.IX.1962 (TRTC-40205). CANADA: *Cain*, Bear Island, Lake Timagami, Ontario, IX.1929 (TRTC-46510); ?*Hamley*, Sherborne Township, Haliburton Co., 1.VIII.1960 (TRTC-36230). MEXICO: *Lemke 39253*, San Luis Potosi, 10 mi W of Xilita, 2.VI.1962 (TRTC); *Cain 36729*, Ciudad del Maiz, San Luis Potosi, 19.VIII. (TRTC). BERMUDA: ?*Seaver & Whetzel 9*, Hungary Bay, 14.I.1926 (NY). U.S.S.R.: *Borysewicz*, Kiev, 15.VIII.1925 (PR-728139). CZECHOSLOVAKIA: *Svrcek*, Divoka Sarka, 3.VIII.1948 (PR-728145); *Velenovsky*, Radohn, VI.1927 (associated with *Lasiobolus ciliatus*, PR-151713); *Velenovsky*, Struhavev, VI.1934 (type of *Lasiobolus leporinus*, PR-152173); *Velenovsky*, Strancice, IX.1926 (type of *Lasiobolus cuniculi*, PR-148664); *Svrcek*, Jetricovice, Hrensko, Goliste Mountains, 11.VII.1969 (PR-685311); *Velenovsky*, Strancice, IX.1938 (PR-151714); *Svrcek*, Jetricovice, Hrensko, Goliste Mountains, 11.VII.1969 (PR-685307); *Velenovsky*, Mnichovice, VII.1928 (lectotype of *Lasiobolus cuniculi*, PR-152169); *Kubicka & Svrcek*, Belanske Tatry Mountains, 22.VII.1958 (associated with *Lasiobolus diversisporus*, PR-728125). GERMANY: *Sydow 1468*, Grunewald, near Berlin, VI.1887 (NY); *Rehm 103 b*, Oetz, Tyrol, VIII.1872 (NY). SWITZERLAND: *Cain*, Graubunden, Fluelpass, E of Davos-Dorf, 1.IX.1971 (TRTC-46412). FRANCE: *Desmazieres 1743*, s. loc., s. dat. (NY).

COMMENTS: *Lasiobolus cuniculi* is close to *L. ciliatus*, but it has broader asci and narrower setae. We examined the lectotype of *L. brachytrichus* (PR-152169), which is very scanty. No asci could be found, but the setae and ascospores did not differ from *L. cuniculi*. In another specimen of *L. brachytrichus* (PR-152170) we found apothecia of *Cheilymenia stercorea*. This may account for the “setae inferiores saepe stellatim ramosae” of Velenovsky’s description of *L. brachytrichus*. We also revised the type specimen

of *L. leporinus* (PR-152173), which is definitively identical with *L. cuniculi*.

- (4) *Lasiobolus diversisporus* (Fckl.) Sacc., Syll. Fung. 8: 538. 1889. Figs. 4, 26
 ≡ *Ascobolus diversisporus* Fckl. in Jb. Nassau. Ver. Naturk. 23-34: 289. 1870.
 ≡ *Humaria diversispora* (Fckl.) Speg. in Michelia, I: 236. 1878.

Apothecia gregarious, sessile, 300-800 μ diam. Disc flat, concolorous with the receptacle, without distinct margins. Receptacle subglobose when young, cupulate at maturity, setose, yellow-orange; anchoring hyphae, subhyaline, non-septate, unbranched, 3-6 μ diam. Setae arising superficially from the lower and median part of the receptacle, non-septate, stiff, straight, pointed, ventricose, 180-492 μ long by 15-42 μ diam at the widest part; walls smooth, uniform, 3-6 μ thick. Ectal excipulum of small, elongated or lobed, 6-11 \times 5.5-6.0 μ , horizontally oriented cells, a textura epidermoidea. Medullary excipulum of delicate, hyaline, narrow cells. Sub-

hymenium inconspicuous. Hymenium multi-ascal, I(-). Asci clavate, rounded or truncate above, attenuate below, short-stalked, 140-234 \times 24-36 μ , eight-spored. Ascospores obliquely uniseriate or biseriata, hyaline to yellowish, ellipsoidal, rounded at both ends, smooth-walled, (21.0-)24.0-34.5 \times 12.0-17.0(-19.5) μ each with a distinct deBary bubble. Paraphysis hyaline, filiform, septate, sometimes branched, slightly inflated to 2.5-3.0 μ diam at their apices.

HABITAT: On dung of cow, horse, deer, ass, and goat.

NAME: Referring to the variable size of ascospores.

SPECIMENS EXAMINED: UNITED STATES: *Luck-Allen*, Big Horn Mountain, Granite Pass, Wyoming, 2.IX.1962 (TRTC-46640); *unknown collector*, s. loc., s. dat. (from the herb. of George Masee, NY). CANADA: *Cain 30141*, Nashville, York Co., Ontario, 9.V.1954 (TRTC). PARAGUAY: *Spegazzini*, Asuncion, s. dat., (LPS-26152); *Spegazzini*, Asuncion, X.1919 (LPS-26153). ARGENTINA: *Spegazzini*, Capital, 5.V.1880 (LPS-26156); *Spegazzini*, La Plata, 28.VI.1885 (LPS-26151); *Spegazzini*, s. loc., s. dat., (TRTC-6838). CHILE: *Spegazzini*, Los Perales, s. dat., (LPS-26155). CZECHOSLOVAKIA: *Kubicka & Svrcek*, Belanske Tatry Mountains, 22.VII.1958 (PR-728125); *Svrcek*, Zdice, 1.V.1949 (PR-728128). SWITZERLAND: *Winter 564*, Cresta Mora Mountain, Albula Pass, VIII.1888 (CUP-10996). GERMANY: *Rehm 103 a*, Lizen, Tyrol, VIII.1872 (NY); *Fuckel 1297*, Frankensteiner Kopf, s. dat. (type locality, NY, UC-70645 A).

COMMENTS: As pointed out by Rifai (1968) this species has larger ascospores than *Lasiobolus ciliatus*. Unlike other congeneric species, this one also shows a tendency to have colored ascospores.

- (5) *Lasiobolus intermedius* Bezerra & Kimbrough spec. nov. Figs. 5, 15

Apothecia gregaria ad congesta, sessilia, 210-465 μ lata, disco plano, aspero, flavo, immarginato. Receptaculum obconicum ad turbinaatum, flavum, setosum, ad substratum hyphis subhyalinis ad olivaceis, esseptatis, 3-6 μ diam affixis. Setae non septatae, rectae, rigidae, acuminatae, simplices, basin subventricosae, parietibus 2-3 μ crassis, cyanophilis granulis ornatae vel non, 200-522 \times 12-30 μ . Excipulum ectale e cellulis elongatis vel lobulatis, horizontalibus,

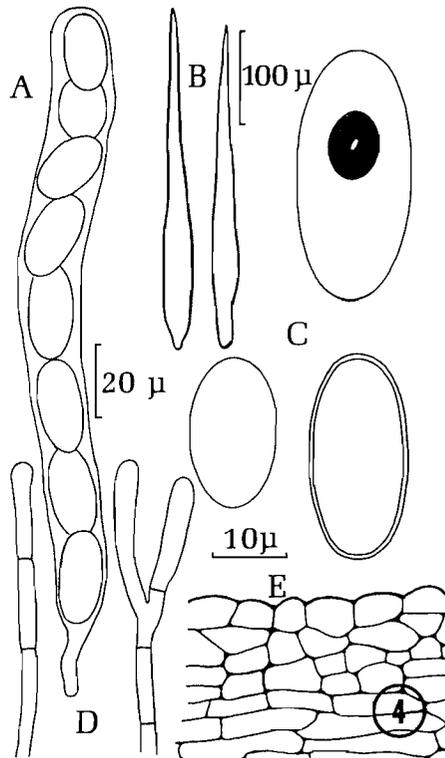


FIG. 4. *Lasiobolus diversisporus*. A. Ascus and ascospores. B. Setae. C. Ascospores, one with a deBary bubble. D. Paraphyses. E. Ectal cells.

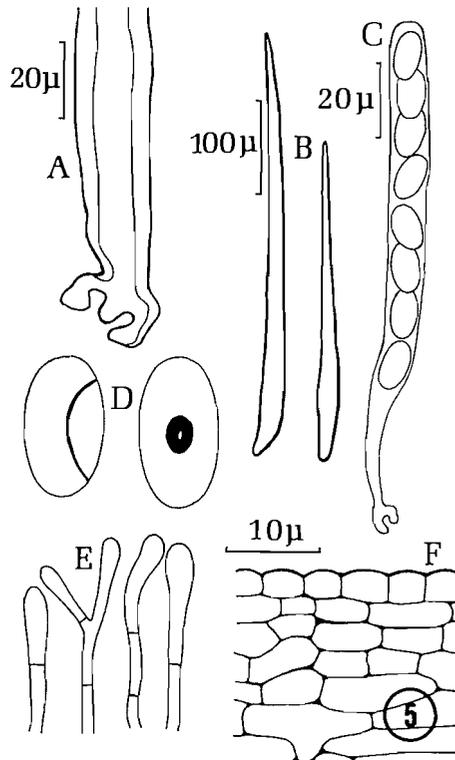


FIG. 5. *Lasiobolus intermedius*. A. Seta base. B. Setae. C. Ascus and ascospores. D. Ascospores, one with a deBary bubble. E. Paraphyses apices. F. Ectal cells.

4.0–26.0 × 2.7–7.0 µ (textura epidermoidea), excipulum medullare e cellulis angustis, hyalinis, compositum. Asci octospori, clavati ad cylindracei, ad apicem rotundati vel truncati, ad basem attenuati, pedicelati, (90–)120–160(–180) × 14–20 µ, jodo non caerulescentes. Ascospores unicellulares, hyalinae, ellipsoideae, uniseriatae, raro superne biseriatae, utrinque rotundatae, laeves, 13.0–18.0 × 7.5–11.5 µ, “de Bary bubble” praeditae. Paraphyses hyalinae, filiformes, septatae, simplices vel ramosae, supernae subincrassatae usque 2–3 µ diam.

Apothecia gregarious to crowded, sessile, 210–465 µ diam. Disc flat, rough, yellow, without margins. Receptacle obconical to turbinate, concolorous with the disc, setose; anchoring hyphae sybhyaline to olive brown, non-septate, unbranched, 3–6 µ diam. Setae arising from lower and median region of the receptacle, non-septate, stiff, pointed, slightly ventricose at their bases, 200–522 µ long by 12–30 µ diam at the widest part; wall smooth or sometimes with cyano-

philous markings, 2–3 µ thick. Ectal excipulum of elongate, lobed, horizontally arranged cells, 4.0–26.0 × 2.5–7.0 µ, a textura epidermoidea. Medullary excipulum of hyaline, narrow cells. Subhymenium inconspicuous. Hymenium multi-ascal, I(–). Asci clavate cylindrical, rounded or truncate above, attenuate below, stalked, (90–)120–160(–180) × 14–20 µ, eight-spored. Ascospores uniseriate to biseriata above, hyaline, ellipsoidal, rounded at both ends, often collapsed at one side, smooth-walled, 13.0–18.0 × 7.5–11.5 µ, each with a prominent deBary bubble. Paraphyses hyaline, filiform, septate, simple or branched, slightly inflated to 2–3 µ diam at their apices.

HABITAT: On dung of moose, horse, deer, elk, opossum, sheep, musk ox, and porcupine.

NAME: Referring to the intermediate-sized spores as compared with large-spored species like *Lasiobolus ciliatus* and *L. diversisporus* and small-spored species such as *L. microsporus* and *L. trichoboloides*.

SPECIMENS EXAMINED: UNITED STATES: F. E. & E. S. Clements, 122, Dark Canyon, Colorado, 3.IX.1904 (NY); Cain 39912, Targhee Pass, Fremont Co., Idaho, 1.IX.1962 (TRTC); Cain 42118, Yellowstone Natl. Pk., Sylvan Pass, Wyoming, 1.IX.1962 (TRTC); Luck-Allen, Washington Olympic Natl. Pk., Elwha River Campsite, 21.VIII.1962 (TRTC-46648). CANADA: Cain 41650, Chafey Locks, Seeds Co., Ontario (TRTC); Cain, S of Wawa, Algoma D., Ontario, 19.VI.1961 (TRTC-46529); Cain, Univ. of Toronto Forest, Muskoka D., Ontario, 17.IX.1965 (TRTC-46533); Luck-Allen 43506, Thunder Bay D., Ontario, 6.VIII.1965 (type of *Lasiobolus intermedius*, TRTC); Cain 41646, Thunder Bay D., Ontario, 6.VIII.1965 (TRTC); Cain 37538, Algoma D., Ontario, 22.VI.1961 (TRTC); Obrist 37266, Toronto, Ontario, 19.XI.1959 (TRTC); Cain et al. 37549, Algoma D., Ontario, 20.VI.1961 (TRTC); Cain 12002, Costello Lake, Ontario, 7.VII.1939 (TRTC-46521); Cain 2702, Timagami Lake, Ontario, 10.VIII.1931 (TRTC); Rogerson, Gatineau Co., Quebec, 1.IX.1959 (NY); Cain 41643, Thunder Bay D., Ontario, 21.VI.1963 (TRTC); Cain, Ontario, s. dat. (TRTC-37568). SWEDEN: Lundquist, Vange, Uppland, 14.IV.1959 (TRTC). SWITZERLAND: Cain, Graubunden, Fluelapass, 29.VIII.1971 (TRTC-46420); Cain, Graubunden, Albula Pass, 29.VIII.1973 (TRTC-46446); Cain, Graubunden, Susch, 1.IX.1971 (TRTC-46398). NEW ZEALAND:

Bell 120, Orongorongo Valley, I.1973 (FLAS-F49584).

COMMENTS: This species probably has been mistaken for *Lasiobolus ciliatus* by many authors despite the overall smaller size of its structures. It probably corresponds to Heimerl's (1889) forms 1 and 2 of *Ascophanus pilosus*. *Lasiobolus minimus* Vel. and *L. vaccinus* Vel. could be used perhaps instead of a new name, but because of their very incomplete descriptions and lack of type specimens, they must be regarded as *nomina dubia*.

(6) *Lasiobolus lasioboloides* March., Mem. Soc. Bot. Belgique, 24: 68-69. 1885. Figs. 6, 17

Apothecia scattered to gregarious, sessile, (210-)300-750 μ diam. Disc convex or flat, whitish to yellow, without margins. Receptacle at first globose, then pulvinate, concolorous with the disc; anchoring hyphae subhyaline, non-septate, unbranched, 2.5-3.0 μ diam. Setae arising superficially from the lower and median parts of the receptacle, non-septate, stiff, straight, acute, non-

ventricose, acicular, (25-)65-192 μ long by 5-9 μ diam at the widest part; walls smooth, 2-3 μ thick. Ectal excipulum of small, elongated, lobed, horizontally arranged cells, 4-14 \times 4-6 μ , a textura epidermoidea. Medullary excipulum of delicate, hyaline cells. Subhymenium inconspicuous. Hymenium multiascal, I(-). Asci clavate cylindrical, rounded above, attenuate below, short pedicelate, 75-115 \times 18-30 μ , eight-spored. Ascospores biseriata, hyaline, broad ellipsoidal to almost subglobose, rounded at both ends, smooth-walled, 13-18 \times 9-13.5 μ , each with a deBary bubble. Paraphyses hyaline, filiform, septate, sometimes branched, slightly inflated to 1.5-2.0 μ diam at their apices.

HABITAT: On dung of moose, deer, rat, elk, sheep, wapiti, and goat.

NAME: Appearing like a *Lasiobolus*.

SPECIMENS EXAMINED: UNITED STATES: Colorado: *Cain* 41657, Rocky Mountains National Park, Larimer Co., 19.VIII.1957 (TRTC); *Cain* 41659, Rocky Mountains National Park, Larimer Co., 19.VIII.1957 (TRTC); *Cain*, Gore Pass, Grand Co., 20.VIII.1957 (TRTC-46641). Wyoming: *Cain* 43907, Shell Canyon, Big Horn Co., 2.IX.1962 (TRTC); *Luck-Allen* 40417, Shell Canyon, Big Horn Co., 2.IX.1962 (TRTC); *Luck-Allen* 40401, Shell Canyon, Big Horn Co., 2.IX.1969 (TRTC); *Luck-Allen* 42109, Upper Shell Canyon, Big Horn Co., 2.IX.1962 (TRTC); *Luck-Allen* 43883, Upper Shell Canyon, Big Horn Co., 2.IX.1962 (TRTC); *Cain* 43456, Nash Fork, W of Centennial, Albany Co., 19.IX.1964 (TRTC). Oregon: *Luck-Allen* 40432, W of Sisters, Deschutes Co., 30.VIII.1962 (TRTC). CANADA: *Guiccionne* 43772, Kananaski Valley, Dutch Creek, Alberta, VIII.1965 (TRTC); ?*Luck-Allen* 38849, Sunwapta Pass, Parker Trail, Alta, 9.VIII.1962 (TRTC).

(7) *Lasiobolus macrotrichus* Rea, Trans. Br. Mycol. Soc. 16: 440. 1917.

Figs. 7, 16, 19, 20, 24
=*Lasiobolus longisetosus* Povah, Pap. Mich. Acad. Sci., Arts Lett. 9: 258. 1929.

Apothecia gregarious to crowded, sessile, (300-) 420-800 (-1000) μ diam. Disc flat, without distinct margins, pale orange to tan. Receptacle obconical to funnel-shaped, setose, concolorous with the disc; anchoring hyphae subhyaline, non-septate, unbranched, 3.0-5.5 μ diam. Setae arising superficially from the lower and median parts of the receptacle, non-septate, bristly,

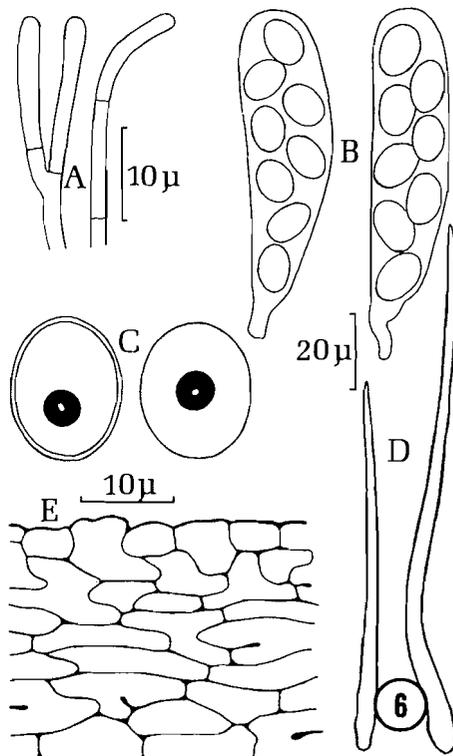


FIG. 6. *Lasiobolus lasioboloides*. A. Paraphyses apices. B. Asci and ascospores. C. Ascospores with deBary bubbles. D. Setae. E. Ectal cells.

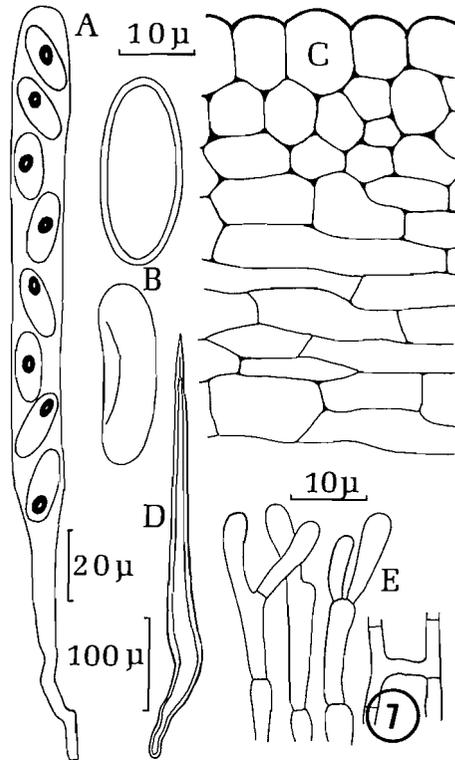


FIG. 7. *Lasiobolus macrotrichus*. A. Ascus and ascospores with deBary bubbles. B. Ascospores. C. Ectal cells. D. Seta. E. Paraphyses apices, two laterally anastomosed.

straight, pointed, ventricose, 300–1000(–1380) μ long by 20–48 μ diam at the widest part; walls smooth, 3.0–7.5 μ thick. Ectal excipulum of small, elongated, sometimes lobed, horizontally arranged cells, 6.5–20.0 \times 3.0–7.5 μ , a textura epidermoidea. Medullary excipulum of hyaline, narrow cells. Subhymenium inconspicuous. Hymenium multiascal, I(–). Asci cylindrical, rounded or truncate above, attenuate below, usually long pedicelate, 110–240 \times 15–27 μ , eight-spored. Ascospores obliquely uniseriate, hyaline, ellipsoidal, rounded at both ends, smooth-walled, (15–)17–22(–24) \times (5.5–)9.0–12.0(–13.5) μ , each with a conspicuous deBary bubble. Paraphyses hyaline, filiform, septate, branched, slightly inflated to 2–3 μ diam at their apices.

HABITAT: On dung of various animals.

NAME: Referring to the long setae.

SPECIMENS EXAMINED (the number of specimens examined for each country or American state is in parenthesis; only a few of these are cited):

UNITED STATES (26): New York (12): *Peck*, Sand-lake, s. dat. (NY); *Smith & Rogerson*, St. Huberts Woods, Essex Co., 17.VI.1958 (NY); *C.J.A.P. 1095*, Adirondack Mts., s. dat. (NY); *Luck-Allen 37380*, Stoddard Brook, Allegany St. Pk., 11.VI.1961 (TRTC); *Mirza*, Utsayantha Mt., Delaware Co., 22.IX.1963 (TRTC); *Rogerson*, Luce Co., near Lower Falls, Tahquamenon River, 3.VIII.1964 (NY). Pennsylvania (3): *Seaver 70*, Center Co., near Meadows, 12.VI.1920 (NY); *Seaver 70*, Huntingdon Co., 13.VI.1920 (NY); *Stitey 49*, Pocono Lake, VIII.1936 (NY). Michigan (4): *Rogerson*, Cheboygan Co., near Douglas Lake, University of Michigan Biological Station, 2.VIII.1964 (NY); *Povah*, Rock River, 9.XII.1927 (CUP-37127, authentic specimen of *Lasiobolus longisetosus*). Wyoming (5): *Cain 32303*, Togwotee Pass, Shoshone Natl. Forest, 2.VII.1955 (TRTC); *Cain 32054*, Togwotee Pass, Shoshone Natl. Forest, 2.VII.1955 (TRTC). Montana (1): *Cummins 74*, Bigfork, 20.VIII.1929 (NY). CANADA (81): *Smith*, South of Timagami, Ontario, 22.V.1960 (TRTC-46651); *Hamley 36315*, Kawagana Lake, Haliburton, Ontario, 22.VIII.1960 (TRTC); *Frances 34977*, Gallapo Marsh, Algonquin Pk., Ontario, 13.IX.1959 (TRTC); *Cain et al. 37531*, Nickel Township, Algoma D., 21.VI.1961 (TRTC); *Luck-Allen 43596*, Hatton Co., S of Ballenafad, Ontario, 12.X.1964 (TRTC); *Krug 39896*, University of Toronto Forest, Muskoka D., Ontario, 28.V.1963 (TRTC); *Cain & Luck-Allen*, SE of Nobleton, York Co., Ontario, 21.V.1967 (TRTC-46534). CZECHOSLOVAKIA (12): *Kavina*, Svata Dobrotiva, 21.VII.1921 (PR-728137); *Svrcek*, Bohemia merid., "Sobeslavska Blata," 1.IX.1950 (PR-728146); *Svrcek & Gulden*, Bohemia merid., Tabor, 17.V.1965 (PR-604051); *Raitviir 52*, Rakvere D., Karepa, 18.VIII.1957 (PR-539542). SWEDEN (3): *Aberg 957*, Funbo parish, Fljallnora, 3.IV.1939 (PR-728131); *Nannfeldt*, Gatrikland, Tolfforskoggen, NW of Tolffors, 25.VIII.1950 (UC-69366A). HOLLAND (1): *Feurich*, "Auf Mist vom Rind bei Goda," 1903 (CUP-6867). SWITZERLAND (4): *Cain*, Graubunden, Susch, 1.IX.1971 (TRTC-46404); *Cain*, Graubunden, Albula Pass, 29.VIII.1971 (TRTC-46444). NEW ZEALAND (1): *Bell 59*, Luxmort, near Lake Te Anau, S Island, I.1973 (FLAS-F49585).

(8) *Lasiobolus microsporus* Bezerra & Kimbrough sp. nov. Figs. 8, 14
Apothecia disseminata ad congesta, sessilia,

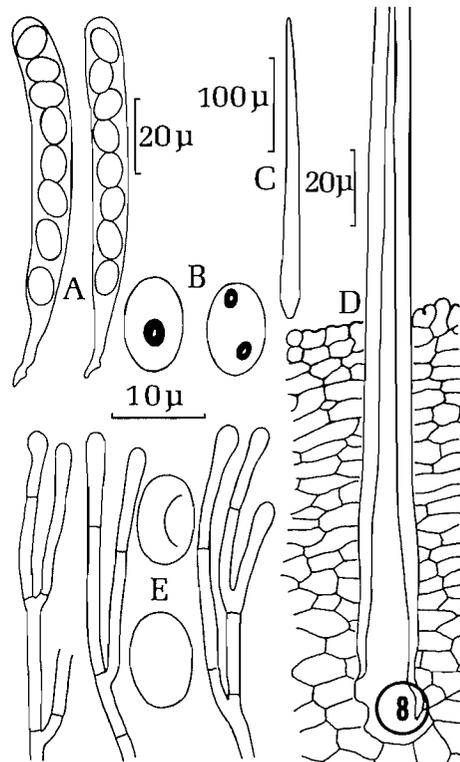


FIG. 8. *Lasiobolus microsporus*. A. Asci and ascospores. B. Ascospores with deBary bubbles. C. Seta. D. Ectal cells and seta attachment. E. Branched paraphyses and ascospores.

350–750 μ lata, disco concavo vel plano, subalbo, immarginato. Receptaculum primo subglobosum deinde obconicum, denique cupulatum, flavum setosum, ad substratum hyphis subhyalinis vel subflavis, eseptatis, 2.5–4.0 μ diam affixis. Setae non septatae, rectae, rigidae, acuminatae, simplices, basin bulbosae, 180–377 \times 10–24(–30) μ , parietibus 3–5 μ crassis, cyanophilis granulis semper ornatae. Excipulum ectale e cellulis parvis, elongatis, angularibus, horizontalibus, 15–20(–30) \times 3–8(–12) μ (textura epidermoidea ad prismatica) ad basem e cellulis isodiametralibus, 10–15 μ diam (textura angulari), excipulum medullare e cellulis angustis, delicatis, hyalinis, compositum. Asci octospori, cylindracei, ad apicem rotundati vel truncati, ad basem attenuati, pedicelati, 90–150 \times 11–12 μ , jodo non caerulescentes. Ascosporae ellipsoideae, hyalinae, uniseriatae, utrinque rotundatae, laeves, 9–11 \times 6.6–8.0 μ “de Bary bubble” praeditae. Paraphyses simplices vel ramosae,

septatae, filiformes, superne incrassatae usque 2.5–5.0 μ diam, hyaline.

Apothecia scattered to gregarious, sessile, 350–750 μ diam. Disc concave or flat, whitish, without distinct margins. Receptacle at first subglobose then obconical and finally cupulate, setose, yellow, rooted to the substratum by non-septate, unbranched, subhyaline to yellowish hyphae, 2.5–4.0 μ diam. Setae originating superficially from the basal and median part of the receptacle, non-septate, stiff, straight, acute, base bulbous, 180–377 μ long by 10–24(–30) μ diam at the widest part; walls 3–5 μ thick, incrustated consistently with cyanophilous markings. Ectal excipulum of small, angular, elongated, 5–20(–30) \times 3–8(–12) μ , horizontally oriented cells, a textura between epidermoidea and prismatica; towards the base the ectal cells become larger, isodiametric, 10–15 μ diam giving rise to a textura angularis. Medullary excipulum of narrow, delicate, hyaline cells. Subhymenium inconspicuous. Hymenium multiascal, I(–). Asci cylindrical, rounded or truncate above, gently narrowing into a long stalk, 90–150 \times 11–12 μ , eight-spored. Ascospores uniseriate, hyaline, ellipsoidal, rounded at both ends, smooth-walled, 9–11 \times 6.6–8.0 μ , each with a distinct deBary bubble. Paraphyses hyaline, filiform, septate, sometimes branched, inflated to 2.5–5.0 μ diam at their apices.

HABITAT: On dung of moose, deer, and rabbit.

NAME: Referring to the minute ascospores.

SPECIMENS EXAMINED: CANADA: *Cain* 36544, Fenelon Falls, Victoria, Ontario, 15.IX.1931 (TRTC); *Cain* 32429, Purbrook, Muskoka D., Ontario, 2.IX.1956 (type of *Lasiobolus microsporus*, associated with *L. cainii*, TRTC); *Cain & Jackson* 2702, Lake Timagami, Timagami Island, Ontario, 10.VIII.1931 (TRTC); *Cain*, Lake Timagami, Ontario, 2.IX.1936 (TRTC-46542); *Cain*, S of Magnetawan, Parry Sound D., Ontario, 22.VIII.1955 (TRTC); *Cain*, Costello Lake, Algonquin Park, 30.VIII.1939 (TRTC-46545). WEST INDIES: *Seaver* 751, St. Thomas, 10–17.III.1923 (NY).

COMMENTS: *Lasiobolus cainii* and *L. trichoboloides* have spores of similar size, but the former has multispore asci and the latter has a different type of setae and ectal cells.

This species has ascospores about the size of those of *Lasiobolus hirtellus* (Karst.) Karst. and *L. avicularius* (Karst) Sacc., but because of

completely inadequate descriptions and lack of type specimens these species must be treated as *nomina dubia*.

(9) *Lasiobolus monascus* Kimbrough, Mycologia, 66: 907-918, 1974. Fig. 9

Apothecia scattered to gregarious, small, setose, pyriform, white to slightly yellowish 480-550 μ high, 250-275 μ broad, uniascal. Ectal excipulum a *textura angularis* to *epidermoidea*, composed of two layers of globose cells reaching 20 μ in diam. Setae of two types, those on the upper third of the ascocarp non-septate with a bulbous base, reaching 240-260 μ long; the basal hairs with two septa, reaching 120-200 μ long. Hymenium uniascal, I(-). Asci operculate, multispored, pyriform, 375-450 μ long, 250 μ wide at the base, 175-185 μ wide at the apex, with multilayered walls, the outermost layer positive in Congo red, a thin area marking the operculum, an internal ring at this area visible in lactic acid - cotton blue. Ascospores more

than 500 per ascus, conglobate, thin-walled, hyaline, smooth, without obvious oil droplets, deBary bubbles infrequent, 7.5-8.0 \times 4.5-5.0 μ . Paraphyses thin, filamentous, 1.5 μ in diam, simple or sparingly branched at the apices, forming a thin layer between the ascus and the excipulum, apices forming an epithelial tissue over the protruding asci (description based on Kimbrough 1974).

HABITAT: On dung of rabbit.

NAME: Referring to the single ascus in apothecium.

SPECIMENS EXAMINED: Conway, San Felasco Hammock, Gainesville, Alachua Co., 31.III.1969 (FLAS-F48548).

(10) *Lasiobolus ruber* (Quel.) Sacc., Syll. Fung. 8: 537. 1889. Figs. 10, 23

= *Ascophanus ruber* Quel., Grevillea, 8: 117. 1880.

= *Lasiobolus capreoli* Vel., Monogr. Discom. Bohem. 1: 413. 1934.

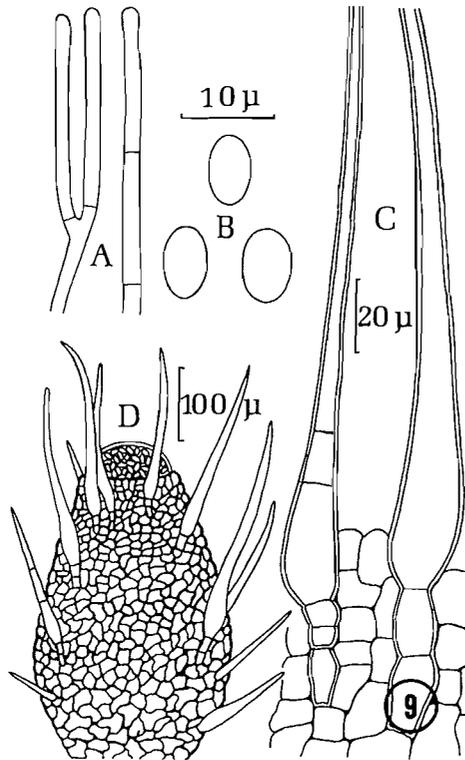


FIG. 9. *Lasiobolus monascus*. A. Paraphyses apices. B. Ascospores. C. Setae attached to ectal cells. D. Apothecium with a single protruding ascus.

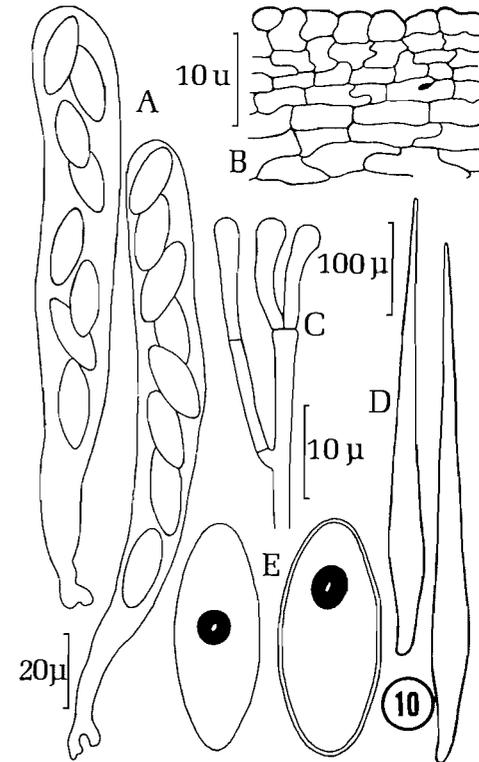


FIG. 10. *Lasiobolus ruber*. A. Asci and ascospores. B. Ectal cells. C. Branched paraphysis. D. Setae. E. Ascospores with deBary bubbles.

Apothecia gregarious, rough, 300–900 μ diam. Disc flat, orange or reddish, without margins. Receptacle at first subglobose, becoming obconical or cupulate, concolorous with the disc, setose; anchoring hyphae subhyaline, non-septate, sparingly branched, 2–3 μ diam. Setae arising from the basal and median parts of the receptacle, non-septate, bristly, acute, ventricose at their bases, 350–825 μ long by 30–48 μ diam at the widest part; walls smooth, 3.0–7.5 μ thick. Ectal excipulum of small, elongated, lobed, horizontally oriented cells, 7.0–10.0 \times 3.0–4.2 μ , a textura epidermoidea. Medullary excipulum of delicate, hyaline, narrow cells. Subhymenium inconspicuous. Hymenium multiascal, I(–). Asci clavate cylindrical, rounded or truncate above, attenuated below, pedicelate, 156–255 \times 18–27 μ , eight-spored. Ascospores uniseriate or biseriate, hyaline, ellipsoidal to almost fusiform, attenuated at both ends, smooth, 22.5–30.0 \times 9.0–13.5 μ , each with an obvious deBary bubble. Paraphyses hyaline, filiform, simple or branched, septate, 1.5–2.0 μ diam below and 4–5 μ diam at their inflated apices.

HABITAT: On dung of cow, deer, wapiti, goat, and wolf.

NAME: Referring to the reddish color of the apothecia.

SPECIMENS EXAMINED: UNITED STATES: *Rogerson*, Cheboygan Co., near Douglas Lake, Univ. of Michigan Biolog. Sta., 2.VII.1964 (NY); *Cain*, Washington Olympic Natl. Pk., Elwha River Campsite, 21.VIII.1962 (TRTC-46649). CZECHOSLOVAKIA: *Svrcek*, Struharov, 28.IV.1945 (PR-728141); *Svrcek*, Hatoky patok, 24.IV.1949 (PR-728147); *Kubicka*, Jirikovo ridoli pr. Salomanovice, 18.V.1965 (PR-604047); *Svrcek*, Trebon, Spalena borkovna Forest, 16.V.1962 (PR-560491); *Kubicka*, Slepici hory Mountains, Kleni, 17.V.1962 (PR-560499); *Velenovsky*, Mni-

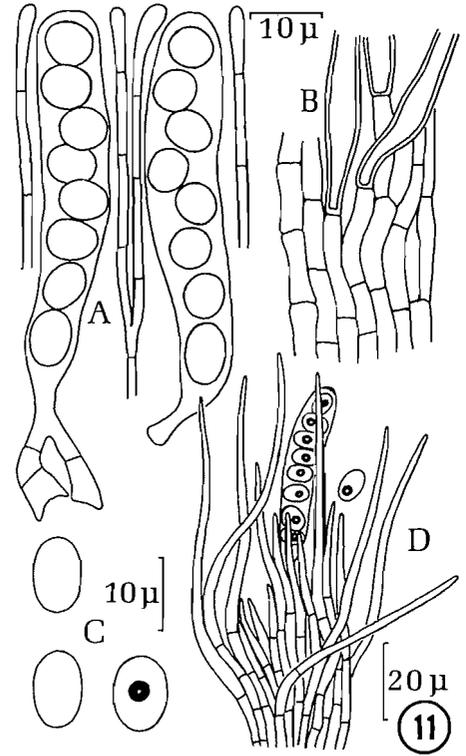


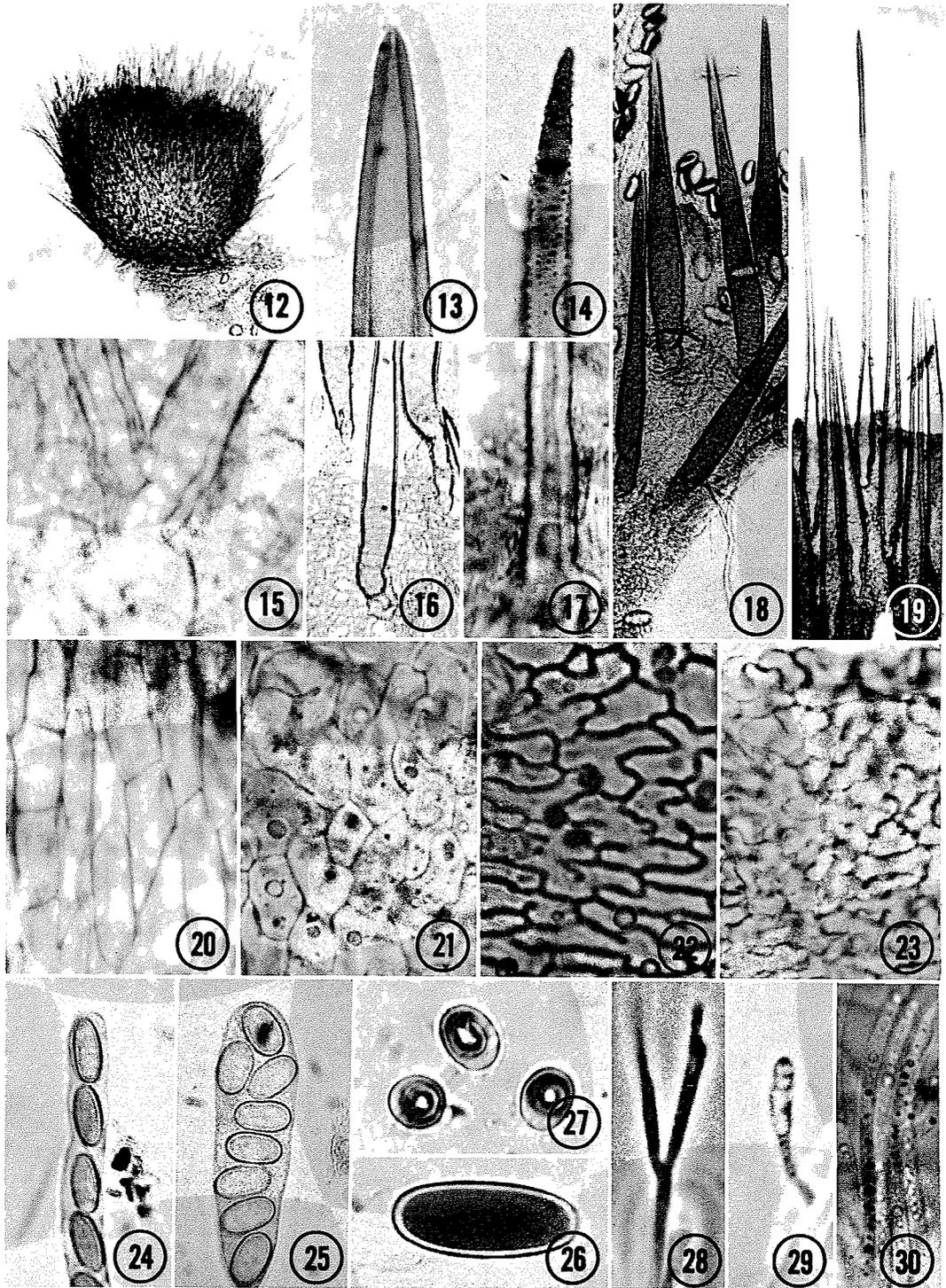
FIG. 11. *Lasiobolus trichoboloides*. A. Asci and paraphyses. B. Ectal cells and setae attachment. C. Ascospores, one with a deBary bubble. D. Setae attached to ectal cells.

chovice, VI.1934 (type of *Lasiobolus capreoli*, PR-152172); *Svrcek*, Cmelice, 7.VIII.1968 (PR-671619); *Svrcek*, Mezna, Hrensko, 1.VII.1969 (PR-685310); *Svrcek*, Mezna Louka, Hrensko, 2.VII.1969 (PR-685309).

(11) *Lasiobolus trichoboloides* Kahn & Bezerra sp. nov. Figs. 11, 12, 27, 29

Apothecia disseminata ad congesta, sessilia, disco plano, aspero, initio albolutescens deinde

Figs. 12–30. Species of *Lasiobolus*. Fig. 12. Apothecium of *L. trichoboloides*. \times 100. Fig. 13. Apex of a hair of *L. ciliatus* with walls staining deeply in Congo red. \times 500. Fig. 14. Apex of hair of *L. microsporus* with cyanophilic markings. \times 500. Fig. 15. An aberrant branched hair of *L. intermedius*. \times 500. Fig. 16. Bases of setae of *L. macrotrichus*. \times 100. Fig. 17. Base of hair of *L. lasioboloides* with atypical septum. \times 1000. Fig. 18. Ventricose setae of *L. ciliatus*. \times 100. Fig. 19. Very long setae of *L. macrotrichus*. \times 100. Fig. 20. Angular ectal cells of *L. macrotrichus*. \times 1000. Fig. 21. Broad, epidermoid ectal cells of *L. cuniculi*. \times 1000. Fig. 22. Elongate, epidermoid ectal cells of *L. ciliatus*. \times 1000. Fig. 23. Small, epidermoid ectal cells of *L. ruber*. \times 1000. Fig. 24. Cylindrical ascus of *L. macrotrichus*. \times 500. Fig. 25. Clavate, cylindrical ascus of *L. cuniculi*. \times 500. Fig. 26. Ascospore of *L. diversisporus* with cyanophilic epispore. \times 1000. Fig. 27. Ascospores of *L. trichoboloides* with deBary bubbles. \times 1000. Fig. 28. Branched paraphyses of *L. cainii*. \times 1000. Fig. 29. Inflated apex of a paraphysis of *L. trichoboloides*. \times 1000. Fig. 30. Paraphyses of *L. ciliatus* showing droplets of carotenoids. \times 1000.



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fulvum, immarginato. Receptaculum cupulatum vel subinfundibuliformes, fulvum, setosum, ad substratum hyphis hyalinis, septatis, 2.0–2.5 μ diam affixis. Setae non septatae vel 1 basilaribus septum praeditae, aciculariformiae ad subcylindraceae, rectae vel curvae, acuminatae, simplices, basin subincrassatae, 50–110 \times 3–5 μ , parietibus 1.0–1.5 μ crassis, laeves. Excipulum ectale e cellulis rectangularibus, verticalibus, 5–24 \times 4.0–8.5 μ (textura prismatica), ad basem e cellulis isodiametralibus, 12–15 μ diam (textura angulari), excipulum medullare e cellulis angustis, delicatis, hyalinis, compositum. Asci octospori, clavati ad cylindracei, ad apicem rotundati, ad basem stricti, pedicelati, 58–88 \times 9–14 μ , jodo non caerulescentes. Ascospores ellipsoideae, hyalinae, uniseriatae, raro superne biseriatae, utrinque rotundatae, laeves, 8.5–11.5 \times 6.0–9.0 μ “de Bary bubble” praeditae. Paraphyses hyalinae, filiformes, septatae, ramosae, superne incrassatae usque 2.5–5.0 μ diam.

Apothecia scattered to gregarious, sessile, small, 150–300 μ diam and 150–255 μ high. Disc flat, rough, at first light yellowish-brown, without distinct margins. Receptacle cupulate or shallow funnel-shaped, setose, concolorous with the disc, setose; anchoring hyphae hyaline, septate hyphae, 2.0–2.5 μ diam. Setae arising superficially from the median and upper part of the receptacle, non-septate or with a basal septum, cylindrical acicular, straight or curved, pointed, with a slightly swollen base, 50–110 μ long by 3–5 μ diam at the widest part; walls smooth, more-or-less uniform, hyaline, 1.0–1.5 μ thick. Ectal excipulum formed by vertically oriented cells with their long axis perpendicular to the surface of the disc, rectangular, 5–24 \times 4.0–8.5 μ , a textura prismatica; towards the base the ectal cells become larger, angular, isodiametric, 12–15 μ diam, forming a textura angularis. Medullary excipulum of hyaline, elongate, delicate cells. Subhymenium inconspicuous. Hymenium multiascal, I(–), 72–102 μ thick. Asci clavate cylindrical, rounded at the apex, gently narrower towards the base then abruptly constricted in a short, sometimes forked, stalk, 58–88 \times 9–14 μ , eight-spored. Ascospores uniseriate or rarely biseriatae above, hyaline, ellipsoidal, rounded at both ends, smooth-walled, 8.5–11.5 \times 6.0–9.0 μ , each with a prominent deBary bubble. Paraphyses hyaline, slender, septate, branched, 1.0–1.5 μ diam below, inflated to 2.5–5.0 μ diam at their apices.

HABITAT: On dung of camel, antelope, goat, cow, and carnivore.

NAME: Looking like *Trichobolus*.

SPECIMENS EXAMINED: UNITED STATES: *Cain* 41657, Larimer Co., Rocky Mountains National Park, Trail Ridge, Colorado, 19.VIII.1957 (associated with *Lasiobolus lasioboloides*, TRTC). MEXICO: *Cain* 37026, Reynosa, Tamaulipas, 20.VIII.1960 (TRTC); *Cain* 36728, Ciudad del Maiz, San Luis Potosi, 19.VIII.1960 (TRTC). KENYA: *Cain et al.*, Lake Amboseli, 18.VIII.1966 (TRTC-661770 q, 111770 r); *Cain et al.*, Lake Amboseli, 18.VIII.1966 (TRTC-661776 f). PAKISTAN: *Wasif*, Karachi, 10.VI.1963 (type of *Lasiobolus trichoboloides*, TRTC-46652); *Ahmed*, Sind Area, 1.IX.1967 (FLAS-F48435).

COMMENTS: The combined characteristics of vertically arranged ectal cells, cylindrical acicular setae, and small ascospores make this species unique in the genus.

Insufficiently Known and Excluded Species

The following list contains those species that do not correspond to the present concept of *Lasiobolus* and those that lack sufficient descriptions and adequate material.

Lasiobolus albicans (Fckl.) Sacc., Syll. Fung. 8: 538. 1889.

BASONYM: *Ascobolus albicans* Fckl., Hedwigia, 5: 3. 1866.

According to Boudier (1907) and Brummelen (1967) this species should be called *Neotiella albicans* (Fckl.) Sacc.

Lasiobolus aurantiaca Batista & Maia, Ann. Soc. Biol. Pernambuco, 13(2): 66. 1955.

From the study of the type specimen and original description there is no doubt that this species is *Scutellinia scutellata* (L. ex St-Amans) Lamb.

Lasiobolus avicularius (Karst.) Karst., Acta Soc. Fauna Fl. Fenn. II, 6: 122. 1885.

BASONYM: *Peziza avicularia* Karst., Not. Sallsk. Fauna Fl. Fenn. Forh. 10: 126. 1869.

Probably similar to *Lasiobolus hirtellus* and *L. microsporus*, but since the description is too incomplete, it should be considered as a *nomen dubium*.

Lasiobolus brachyaschus March., Mem. Soc. R. Bot. Belgique, 24: 73. 1885.

This species is the type of *Cubonia* Sacc., a doubtful genus according to Eckblad (1968).

Lasiobolus dubius Starb., Ark. Bot. 2: 2. 1904.

This species can not be regarded as a *Lasiobolus* because it was described with septate setae and asci turning blue in iodine. The description is insufficient to place it in the proper genus.

Lasiobolus hirtellus Karst., Acta Soc. Fauna Fl. Fenn. II, 6: 122. 1885.

BASONYM: *Ascobolus hirtellus* Karst., Fungi Fenn. No. 657. 1867; P. Karst. in Not. Sallsk. Fauna Fl. Fenn. Forh. 11: 210. 1870.

A small-spored form of *Lasiobolus* with an original description indistinguishable from that of *Lasiobolus avicularius*. Because of the insufficient description, it should be regarded as a *nomen dubium*.

Lasiobolus horrescens Roll., Bull. Soc. Mycol. Fr. 14: 83. 1898.

This species should be removed from *Lasiobolus* because of the type of the ascospore ornamentation. The white, non-septate setae and other features described and depicted in the original paper are suggestive of the genus *Leucoscypha*. The substrata on which this species was found (leaves and sepals) are also wrong for *Lasiobolus*.

Lasiobolus microscopicus (Wallr.) Rehm, Rab. Krypt.-Fl. I(3): 1098. 1895.

BASONYM: *Peziza microscopica* Wallr., Fl. crypt. Germ. 2: 480. 1833.

A *nomen dubium* according to Brummelen (1967).

Lasiobolus minimus Vel., Novitatis mycologicae, p. 203. 1939.

Probably similar to *Lasiobolus intermedius* but should be regarded as a *nomen dubium* because of the very incomplete description and lack of a type specimen.

Lasiobolus oligotrichus Smith, Trans. Br. Mycol. Soc. 5: 238. 1916.

Somewhat similar to *Lasiobolus cuniculi* judging from the very poor original description. It should be regarded as a *nomen dubium*.

Lasiobolus pulcherrimus (Crouan) Schroet., Krypt.-Fl. Schl. (Edited by Cohn.), 3(2): 54. 1893.

BASONYM: *Ascobolus pulcherrimus* Crouan, Ann. Sci. Nat. (Bot.) IV, 10: 196. 1858.

Le Gal (1961), who revised Crouan's original specimens, accepted Schroeter's combination.

Brummelen (1967) was unable to place the species in any genus. The septate setae and the type of excipulum as depicted by Le Gal (1961) are not typical of *Lasiobolus*. *Cheilymenia* is probably a better genus to accommodate this species.

Lasiobolus raripilus (Phill.) Sacc., Syll. Fung. 8: 537. 1889.

BASONYM: *Ascobolus raripilus* Phill., Grevillea, 7: 23. 1878.

Dennis (1960b) and Rifai (1968) consider this species as a *Cheilymenia*.

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