

A REDELIMITATION OF THE SPECIES OF PILOBOLUS

HU Fu-meì ZHENG Ru-yong CHEN Gui-qing

Systematic Mycology & Lichenology Laboratory
Institute of Microbiology, Academia Sinica, Beijing

ABSTRACT: Nine species of *Pilobolus* were accepted by Zheng & Hu (in Tai, 1979). All of these were collected and studied recently. Though they are distinguishable from each other, in this paper they are redelimited as five species comprising nine varieties in order to achieve concordance with the other genera of the Mucorales where the existing species concept for classifying *Pilobolus*, including ours in the past, is too small and needs revising. The taxa now accepted are: *Pilobolus crystallinus* (Wigg.) Tode var. *crystallinus*; *P. crystallinus* var. *hyalosporus* (Boedijn) Hu & Zheng, comb. nov.; *P. crystallinus* var. *kleinii* (van Tieghem) Zheng & G.-q. Chen, comb. nov.; *P. lentiger* Corda var. *lentiger*; *P. lentiger* var. *minutus* (Speg.) Zheng & G.-q. Chen, comb. nov.; *P. longipes* van Tieghem; *P. oedipus* Mont.; *P. roridus* (Bolt.) Pers. var. *roridus*; *P. roridus* var. *umbonatus* (Buller) Hu & Zheng, comb. nov. A study of the diagnoses given in the literature of some synonyms, which were referred to different taxa by different authors, was made to determine their correct placement. Twelve names are listed here as doubtful since no diagnoses could be found or no conclusion could be drawn from the diagnoses. These include: *Mucor obliquus* Scop., *M. urceolatus* Dicks., *Pilobolus urceolatus* Purt., *P. pestis-bovinae* Hallier (= *P. hallierii* Rivolta), *P. nanus* van Tieghem, *P. intermedius* (Coem.) P. A. Karsten (= *P. oedipus* var. *intermedius* Coem.), *P. pullus* Masee, *P. proliferens* McVickar, *P. ramosus* McVickar, *P. simplex* McVickar, *P. lentiger* forma *kleinii* Reyn. & Laysa, and *P. lentiger* forma *minutus* Reyn. & Laysa.

KEY WORDS: *Pilobolus*; Pilobolaceae; Mucorales; fungi; taxonomy

The Pilobolaceae is a small family of the Mucorales, differing from other families of the order by possessing sporangia which are hemispherical, cutinized, and may be forcibly discharged or detached as a whole, as well as possessing special structures such as subsporangial swellings and trophocysts. The family was established by Corda (1837) based on the genus *Pilobolus* Tode (1784). Except for a very few authors, such as Zycha (1935), Zycha, Siepmann & Linnemann (1969) who accommodated all genera of the Pilobolaceae in the Mucoraceae, most mycologists working on the Mucorales agree that this family should be separated from the other families in the order (Lendner, 1908; Naumov, 1939, 1954; Hesseltine, 1950, 1952; Boedijn, 1958; Hesseltine & Ellis, 1973; Milko, 1974; Benjamin, 1979; Mikawa, 1979; Benny, 1982).

Three genera have been generally accepted in the family: *Pilobolus*, *Pilaira* van Tieghem, and *Utharomyces* Boedijn. Both *Pilobolus* and *Utharomyces* possess a subsporangial swelling and trophocyst, but sporangia of *Pilobolus* are violently discharged

whilst those of *Utharomyces* are not. *Pilaira* has neither a subsporangial swelling nor trophocyst, and its sporangia also are not forcibly discharged. The teleomorph of *Utharomyces* has not yet been found. Zygosporangia of *Pilobolus* and *Pilaira* are smooth and formed between tong-shaped suspensors. Benjamin & Hesseltine (1959) and Hesseltine & Ellis (1973) pointed out the close affinity of *Phycomyces* to the Pilobolaceae, while Mikawa (1979) transferred it to that family. Mikawa argued that the zygospores of *Phycomyces* and Pilobolaceae were the same; the swollen cells on the substrate mycelia of *Phycomyces* which he called 'trophocyst-like cells' were considered homologous to the trophocysts of the Pilobolaceae. He claimed that the absence of cutinized sporangia of *Phycomyces* should not be taken as a ground to exclude it from the Pilobolaceae. This treatment was not followed by other authors. In our opinion, the three known genera of the family Pilobolaceae comprise a very natural group of fungi, their teleomorphs where known are the same and their anamorphs are also very similar in many aspects, especially the cutinization of sporangia and the method of spore release. They are quite distinct from *Phycomyces*, however, which does not produce zygospores on opposed suspensors and should not be retained in the Mucoraceae; perhaps it is better to follow von Arx (1982) and to place it together with *Spinellus* in his new family Phycomycetaceae.

All members of the family are coprophilous. The genus *Pilobolus* has been studied more extensively, especially on its mechanism of phototropism. Fungi of the Pilobolaceae were thought to be of no economic importance until recently, when Gronvold & Jorgensen (1987) proved by experiments that *Pilobolus kleinii* could be responsible for the spreading of the lungworm *Dictyocaulus viviporus* through the discharge of sporangia carrying lungworm larvae from faeces of diseased calves onto the feeds of healthy ones.

More than fifty names of *Pilobolus* species have been published, with seven to nine species generally recognized, all found in China. Four or five species were reported in *Pilaira*, none of which has been recorded in our country. *Utharomyces* has only one species but this has been reported many times including once from Taiwan Province (Kirk & Benny, 1980).

Though *Pilobolus* species can be easily grown on artificial media, they are difficult to preserve either as living cultures or as dried specimens and no type specimens could be obtained for direct study. Moreover, the diagnoses of most of the species published are meager, making them very confusing for use in species identification. Different names were often used by different authors for the same species.

Characteristics which can be used for classifying *Pilobolus* species include: the height and width of the sporangiophores; whether the trophocysts are single or in chain; the shape, colour, and size of the trophocysts, subsporangial swellings, sporangia, columellae, and sporangiospores; and the thickness of the spore wall. Among these, the shape of the columellae and the characteristics of the sporangiospores are most important in all species. Though the sizes of individuals are easily affected by environmental factors and may vary greatly within the same species, the range of sizes of a species is still quite constant and may have some use for delimitating species. Other characteristics may be meaningful in one or certain species but meaningless in others.

Grove (1934) exerted the most influence on species delimitation in *Pilobolus*. All authors, including those of China, adopted Grove's system for classifying the genus.

In China, Ou (1940) reported five species of *Pilobolus* from Sichuan Province, namely

Pilobolus crystallinus (Wigg.) Tode, *P. longipes* van Tieghem, *P. oedipus* Mont., *P. lentiger* Corda (as *P. sphaerosporus* (Grove) Palla), and *P. roridus* (Bolt.) Pers. Fang (1941, 1942) reported two of the above species (*P. crystallinus* and *P. lentiger*, also as *P. sphaerosporus*), from the same province. Zheng & Hu (in Tai, 1979) studied dung samples collected from all provinces of China, and reported four more species in addition to the five already known: *P. hyalosporus* Boedijn, *P. kleinii* van Tieghem, *P. morinii* Sacc., and *P. umbonatus* Buller. Beginning in 1987, we collected many dung samples from various provinces and rediscovered all of the species, i.e., 347 *Pilobolus* isolates were obtained from 2190 dung samples and identified as nine taxa, comprising all those accepted by most students of the genus. After a careful restudy, we believe that these taxa are distinguishable, but that the existing species concept for classifying *Pilobolus* is too narrow. In order to achieve concordance with the other genera of the Mucorales, the species are redelimited as follows:

Both *Pilobolus hyalosporus* and *P. kleinii* differ from *P. crystallinus* merely in that the spores of *P. hyalosporus* are broader and paler, while those of *P. kleinii* are larger and deeper in colour. Hence, they are recombined as *P. crystallinus* var. *hyalosporus* and *P. crystallinus* var. *kleinii* respectively.

Pilobolus morinii Sacc. is considered to be synonymous with *P. minutus* Speg. *Pilobolus minutus* was described by Spegazzini in 1880 and reduced to variety by Dewèvre in 1894 as *P. kleinii* var. *minor* Dewèvre, which was listed as a synonym of *P. kleinii* by Grove (1934). Hesseltine (1950) listed *P. minutus* as a doubtful species but stated that "it may have been a small *Pilobolus crystallinus*", while Zycha, Siepmann & Linnemann (1969) treated *P. minutus* as a synonym of *P. oedipus*. Since spores of *Pilobolus minutus* are described as ellipsoid or spherical, and not indicated as thick-walled, it does not seem to have any affinity with *P. kleinii*, *P. crystallinus* or *P. oedipus*. According to their descriptions, *P. morinii* and *P. minutus* are conspecific, although the diameter of the spores of the former is described as 4.5–6 μm and that of the latter 7–8 μm . The Chinese fungus which we published under the name *P. morinii* in SYLLOGE FUNGORUM SINICORUM (Tai, 1979) has a spore measurement of (4.8–)5.4–6.9(–8.6) μm diam., covering those of *P. morinii* and *P. minutus* quite well. *Pilobolus lentiger*, an earlier name of the well known *P. sphaerosporus*, is a species most closely related to both *P. morinii* and *P. minutus*. All of them belong to the small-sized *Pilobolus* species with similar columellae and possess more or less deep yellow coloured, subspherical to spherical spores. The only distinction between *P. lentiger* and *P. minutus* or *P. morinii* is that the spores of *P. lentiger* are larger than those of *P. minutus* or *P. morinii*. Both the latter two are thus reduced to variety and renamed: *P. lentiger* var. *minutus*.

Pilobolus umbonatus differs from *P. roridus* merely in possessing umbonate sporangia, hence it is reduced to a variety of the latter: *Pilobolus roridus* var. *umbonatus*.

Pilobolus longipes is thought to be distinct on the basis of the very large sporangiophores, especially the very long trophocysts which are formed outside, and not inside the substrate like the other species. *Pilobolus oedipus* is also thought to be distinct by possessing a very thick spore wall. In total, five species comprising nine taxa are recognized.

Names of these taxa, either correct names or synonyms, have often been used by different authors for different fungi with the same name. Owing to the difficulty that no type specimens or cultures can be studied, revisions can only be based on their diagnoses or

Table 1. Redelimitation of species in the genus *Pilobolus*

Size of Fructifications	medium 2-12(14) mm				large 11-35 mm	small 1-5 mm			
Columellae									
Spore Shape	ellipsoid				broad ovoid	broad ovoid to subglobose or globose		globose	
Other Characteristics of spores	 4.5-7.5 x 3-4.5 μm		 7-10 x 4.5-6 μm	 10-20 x 5.5-9.5 μm	 6.5-9.5 x 5.5-8.5 μm	 8.5-13.5 x 7.5-12.5 μm	 11-13.5 x 10-12 μm	 (4.5-)-5.5 x 7(-8.5) μm	 8-18.5 μm
Other Characteristics									
Names Universally Used	<i>P. roridus</i>	<i>P. umbonatus</i>	<i>P. crystallinus</i>	<i>P. kleinii</i>	<i>P. hyalosporus</i>	<i>P. longipes</i>	<i>P. oedipus</i>	<i>P. minutus</i> (= <i>P. morinii</i>)	<i>P. lentiger</i> (= <i>P. sphaerosporus</i>)
Names Proposed	<i>P. roridus</i> var. <i>roridus</i>	<i>P. roridus</i> var. <i>umbonatus</i>	<i>P. crystallinus</i> var. <i>crystallinus</i>	<i>P. crystallinus</i> var. <i>kleinii</i>	<i>P. crystallinus</i> var. <i>hyalosporus</i>	<i>P. longipes</i>	<i>P. oedipus</i>	<i>P. lentiger</i> var. <i>minutus</i>	<i>P. lentiger</i> var. <i>lentiger</i>
Species Recognized	<i>P. roridus</i>		<i>P. crystallinus</i>			<i>P. longipes</i>	<i>P. oedipus</i>	<i>P. lentiger</i>	

descriptions. For example, according to Grove (1934), Brefeld's (1881) *Pilobolus crystallinus* should be *P. kleinii*, Cohn's (1851) *P. crystallinus* should be *P. oedipus*, etc. In our list of synonyms, none of such misidentified names is included. Textual research of the diagnoses of some of the synonyms which were referred to different taxa by different authors, has been made in order to determine their correct placement. If no diagnosis can be found, or no conclusion can be drawn from the diagnosis, they are listed as doubtful. For example, *P. schmidtii* Sacc. (1926) was treated as synonymous with *P. roridus* by Hesseltine (1950), but synonymous with *P. crystallinus* by Zycha, Siepmann & Linnemann (1969). According to its diagnosis, it should be placed under *P. crystallinus* since the spores measured $6.5-8.5 \times 5-6 \mu\text{m}$. *Pilobolus argentinus* Speg. was treated as a synonym of *P. oedipus* by Hesseltine (1950), but as a synonym of *P. lentiger* (as *P. sphaerosporus*) by Zycha, Siepmann & Linnemann (1969). According to its diagnosis, it should be placed under *P. oedipus* since the wall of the spore was described as very thick.

Twelve names have been listed as doubtful.

The names *Mucor obliquus* Scop., *M. urceolatus* Dicks., and *Pilobolus urceolatus* Purt., which have often been listed by some authors as synonyms of *P. crystallinus*, are treated as doubtful here because no descriptions are available for study and comparison.

Pilobolus pestis-bovinae Hallier, with its synonym *P. hallierii* Rivolta, was considered to be identical to *P. lentiger* (as *P. kleinii* var. *sphaerosporus*) according to its figure by Fischer (1892). This fungus has not been reported ever since then and its original diagnosis is not detailed enough to distinguish it from the other taxa.

Pilobolus nanus van Tieghem is characterized by having intercalary trophocysts and sporangia with an apophysis and which are persistently yellow coloured. This species has only been reported twice since its publication. Both records were from India, the first by Ginai (1936), and the second by Nand & Mehrotra (1968), which was republished once again without changing a word in 1977 by the same authors in the same journal. Since two of the above mentioned characteristics, viz. the presence of apophyses and intercalary trophocysts, of *P. nanus* were not reflected in Ginai's and Nand & Mehrotra's descriptions, and as intercalary trophocysts and yellow coloured sporangia may be occasionally encountered in other species, it is better to place this fungus among the doubtful species until more are found with such characteristics which can be proved to be stable.

Pilobolus intermedius (Coem.) P. A. Karsten (= *P. oedipus* var. *intermedius* Coem.) is usually treated as a synonym of *P. lentiger*, but the height of its fructifications was described as 2-5 cm and the spores described as thick-walled which makes it seem to be *P. longipes* and not *P. lentiger*. On the other hand, the measurement of spores being $12-17 \times 11-15 \mu\text{m}$, it could neither be *P. longipes* nor *P. lentiger*.

Pilobolus pullus Masee was treated by both Hesseltine (1950) and Zycha, Siepmann & Linnemann (1969) as one of the synonyms of *P. kleinii*, but the length / width ratio of spores of this species of 4.3 is quite different to that of *P. kleinii* which is usually 2:1. It is preferable to refer it to the doubtful species rather than to *P. kleinii*.

The three newly reported species *Pilobolus proliferens* McVickar, *P. ramosus* McVickar, and *P. simplex* McVickar are all treated as doubtful, because, as Hesseltine (1950) has already pointed out, the main characteristics set forth by McVickar (1942) to establish them seem to be variations of *Pilobolus* in culture. Moreover, no measurement

except the size of the spores had been provided in their diagnoses. Even this was not given by range, but merely a simple figure of length and width was mentioned for each species.

Pilobolus lentiger forma *kleinii* (van Tieghem) Reyn. & Laysa and *P. lentiger* forma *minutus* (Speg.) Reyn. & Laysa were published as 'Form *kleinii*' and 'Form *minutus*' under *P. lentiger* for *P. kleinii* and *P. minutus* respectively. The spore measurements given by Reynolds & Laysa (1967) for their forms are respectively $12.4-15.5 \times 21.7-24.8 \mu\text{m}$ and $12.4-15.3 \times 9.3 \mu\text{m}$ and are quite different from those of *P. kleinii* and *P. minutus*. Hence, these names are treated as doubtful here.

All descriptions of the taxa accepted by us are based on our own observation of materials isolated from dung collected from all parts of China. Usually the fructifications studied were isolated directly from dung kept in moist chambers under room temperature (20-30 C) with alteration of light and darkness after being brought to the laboratory. When purification of species or a longer period of study was necessary, the fructifications grown on dung were transferred to rabbit or horse dung extract agar (dried rabbit or horse dung 200 g, agar 13 g, distilled water 1000 ml.) for further study. No zygospores were detected either in original materials or in crosses of many of the strains isolated.

Pilobolus Tode:Fr., Schrift. d. Berl. Gesell. naturf. Freunde 5:46. 1784.

= *Hydrogera* Wigg., Primitiae Florae Holsaticae: 110. 1780.

= *Pycnopodium* Corda, Icon. Fung. 5:18. 1842.

Mycelia formed in the substrate and developed into trophocysts which are separated from the hyphae by septa; trophocysts usually buried in the substratum but sometimes external, mostly turbinate or ovate, sometimes very long, giving rise to a sporangiophore at one end; sporangiophores phototropic, nonseptate, straight to slightly curved, subequal in diameter throughout or more often slightly enlarging upward to form a subsporangial swelling just beneath the sporangium; subsporangial swellings obovoid, elliptic-ovoid or subglobose, usually orange yellow at the base; sporangia usually black, hemispherical, cutinized, forcibly discharged at maturity; columellae formed at the apex of the subsporangial swellings inside the sporangia; sporangiospores single-celled, ellipsoid, subglobose to globose, subhyaline, yellowish to deep yellow. Zygospores in zygosporangia which are subsmooth to somewhat roughened but not verrucose, formed between two equal and tong-shaped suspensors. Heterothallic in all known species. Coprophilous.

TYPE SPECIES: *Pilobolus crystallinus* (Wigg.) Tode var. *crystallinus* (Basionym: *Hydrogera crystallina* Wigg.)

KEY TO SPECIES AND VARIETIES OF PILOBOLUS

1. Spores ellipsoid and not exceeding $7 \mu\text{m}$ in length; columellae plano-convex, not exceeding $110 \mu\text{m}$ in height 2
1. Spores not ellipsoid, if ellipsoid then exceeding $7 \mu\text{m}$ in length; columellae not plano-convex and usually exceeding $110 \mu\text{m}$ in height 3
2. Sporangia not umbonate 5-1. *Pilobolus roridus* var. *roridus*

2. Sporangia umbonate 5-2. *Pilobolus roridus* var. *umbonatus*
3. Spores ellipsoid and exceeding 7 μm in length or broad ovoid; columellae narrowly campanulate; fructifications medium size 2-12(-14) mm high. 4
3. Spores subglobose to globose; columellae conical, not constricted at the middle; fructifications either 11-35 mm high or 1-5 mm high 6
4. Spores 7-10 \times 4.5-6 μm 1-1. *Pilobolus crystallinus* var. *crystallinus*
4. Spores longer or broader 5
5. Spores 6.5-9.5 \times 5.5-8.5 μm , hyaline, at most pale yellowish
- 1-2. *Pilobolus crystallinus* var. *hyalosporus*
5. Spores 10-20 \times 5.5-9.5 μm , deep yellow 1-3. *Pilobolus crystallinus* var. *kleinii*
6. Fructifications large size 11-35 mm high; trophocysts formed outside the substratum, very long, reaching 1730 μm 3. *Pilobolus longipes*
6. Fructifications small size 1-5 mm high; trophocysts formed inside the substratum, not long, usually not exceeding 500 μm 7
7. Spores very thick-walled, broad ovoid, subglobose to globose. 4. *Pilobolus oedipus*
7. Spores thin-walled, globose 8
8. Spores 8-18.5 μm diam. 3-1. *Pilobolus lentiger* var. *lentiger*
8. Spores 5.5-7(-8.5) μm diam. 3-2. *Pilobolus lentiger* var. *minutus*

1-1. *Pilobolus crystallinus* (Wigg.:Fr.) Tode, Schrift. d. Berl. Gesell. naturf. Freunde 5:47. 1784. var. *crystallinus* (Fig. 1)

= *Hydrogera crystallina* Wigg.:Fr., Primitiae Florae Holsaticae:110. 1780.

= *Pilobolus schmidtii* Sacc., Syll. Fung. 24:11. 1926.

Fructifications 5-12 mm high; sporangiophores arising from the trophocysts, erect, unbranched, nonseptate, 70-125 μm wide; trophocysts turbinate, ovate, or subglobose, buried in the substratum, 150-565 \times 150-460 μm ; subsporangial swellings obovoid, orange coloured at the base, 230-930 \times 160-615 μm ; sporangia black, hemispherical, 60-210 \times 120-385 μm ; columellae campanulate, slightly narrowed at the middle, 115-210 \times 130-265 μm , upper portion 70-145 μm diam.; sporangiospores ellipsoid, light yellow, 7.2-10.1 \times 4.4-6.0 μm . Zygospores not found.

NUMBER OF STRAINS STUDIED: 156.

SUBSTRATA: On dung of camels, cows, deers, elephants, foxes, horses, kangaroos, mules, muntjacs, pigs, rabbits, sheep, and other animals.

DISTRIBUTION IN CHINA: Beijing; Fujian: Fuzhou, Xiamen; Guangdong: Guangzhou, Jiangmen; Guangxi: Guilin, Nanning; Guizhou: Guiyang, Puan, Tongren, Yinjiang; Hainan; Hebei: Guyuan, Jixian; Hunan: Changsha; Jiangsu: Nanjing, Shanghai, Yangzhou, Zhenjiang; Nei Menggu: Dalate, Daqingshan; Ningxia: Yinchuan; Shaanxi: Taibaishan; Shandong: Qingdao, Weixian; Shanxi: Taiyuan, Wutaishan, Yongji, Zhongtiaoshan; Sichuan: Chengdu, Peiling; Yunnan: Kunming; Zhejiang: Hangzhou.

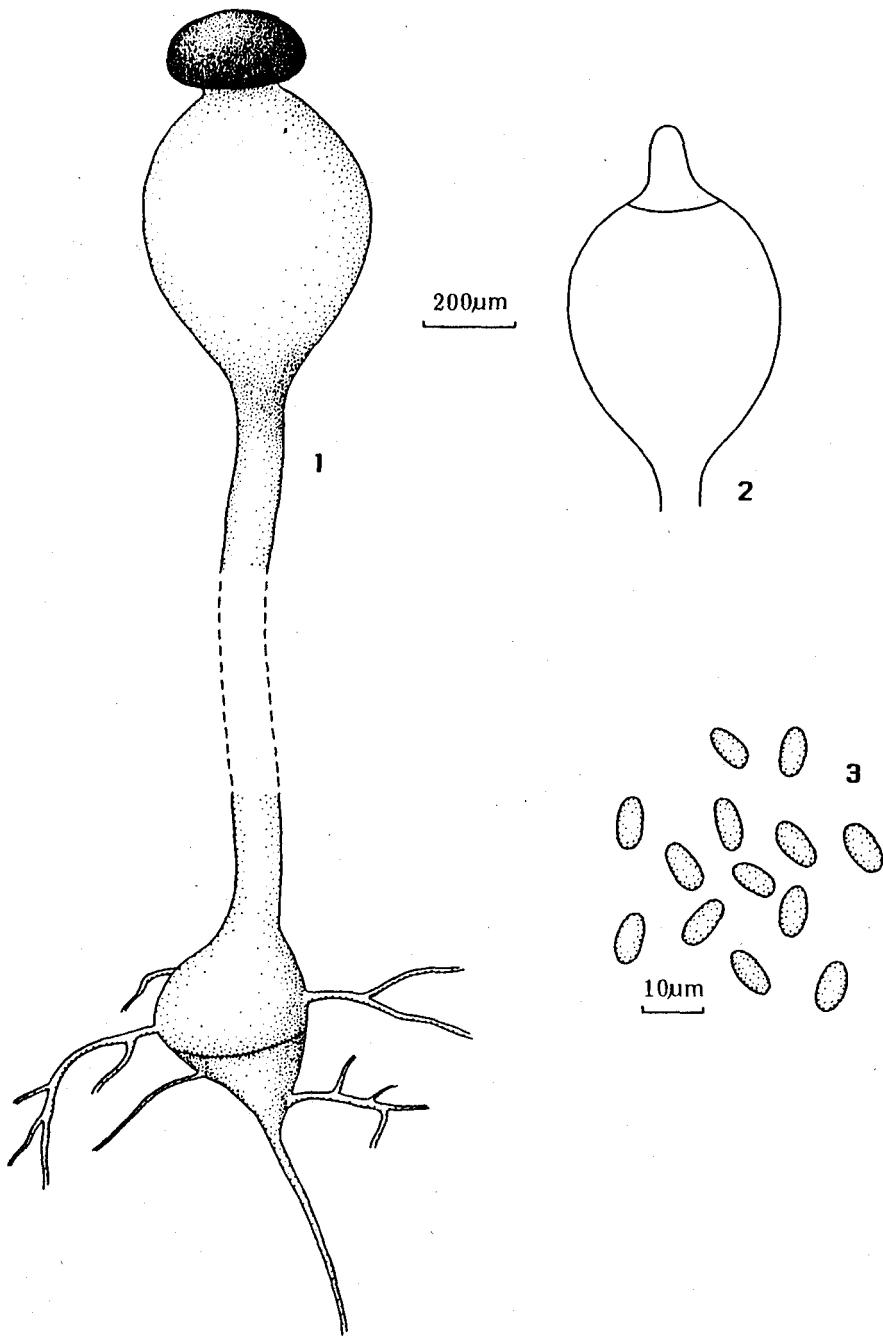


Fig. 1 *Pilobolus crystallinus* var. *crystallinus*. 1. A fructification showing sporangium, subsporangial swelling, sporangiophore, and trophocyst. 2. A subsporangial swelling with a columella. 3. Spores. (Strain P13)

1-2. *Pilobolus crystallinus* var. *hyalosporus* (Boedijn) Hu & Zheng comb. nov. (Fig. 2)

= *Pilobolus hyalosporus* Boedijn, Sydowia 12:340. 1958.

Fructifications 5–10 mm high; sporangiophores arising from the trophocysts, erect, unbranched, nonseptate, 70–165 μm diam. in the upper portion and 40–115 μm diam. in the lower portion; trophocysts ovate to broadly elliptic, buried in the substratum, 200–535 \times 160–460 μm ; subsporangial swellings obovoid, light orange to dirty yellow at the base, 265–845 \times 170–565 μm ; sporangia black, hemispherical, 70–255 \times 145–460 μm ; columellae campanulate, slightly narrowed at the middle, 95–195 μm high, 85–140 μm diam. in the upper portion and 95–230 μm diam. in the lower portion; sporangiospores broadly ovoid to subglobose, subhyaline to pale yellowish, 6.4–9.5 \times 5.5–8.4 μm . Zygospores not found.

NUMBER OF STRAINS STUDIED: 40.

SUBSTRATA: On dung of camels, chickens, cows, deers, donkeys, horses, monkeys, mice, pigs, sheep, and other animals.

DISTRIBUTION IN CHINA: Beijing; Fujian; Fuzhou; Guangdong; Guangzhou; Guangxi; Guilin; Guizhou; Ynjiang; Hebei; Baihuashan, Jixian; Jiangsu; Nanjing, Shanghai, Yangzhou; Nei Menggu; Dalate; Shandong; Qingdao, Taian; Shanxi; Zhongtiaoshan; Yunnan; Kunming; Zhejiang; Hangzhou.

1-3. *Pilobolus crystallinus* var. *kleinii* (van Tieghem) Zheng & G.-q. Chen comb. nov. (Fig. 3)

= *Pilobolus kleinii* van Tieghem, Ann. Sci. Nat. Bot., Ser. VI. 4:337. 1876.

= *Pilobolus roseus* Speg., Anal. Soc. Cient. Argent. 9:175. 1880.

= *Pilobolus heterosporus* Palla, Oesterr. Bot. Zeit. 50:349. 1900.

= *Pilobolus gracilis* Lyr, Arch. Protist. 99:262. 1954. nom. illegit. (not validly published)

= *Pilobolus kleinii* subsp. *hallensis* Lyr, Arch. Protist. 99:270. 1954. nom. illegit. (not validly published)

= *Pilobolus lentiger* forma *heterosporus* (Palla) Reyn. & Laysa, Philipp. Agric. 50:781. 1967.

Fructifications 5–14 mm high; sporangiophores arising from the trophocysts, erect, unbranched, nonseptate, 65–140 μm diam. in the upper portion and 40–85 μm diam. in the lower portion; trophocysts ovate–cylindric or turbinate, buried in the substratum, 140–455 \times 125–295 μm ; subsporangial swellings obovoid, orange–yellow at the base, 295–905 \times 220–520 μm ; sporangia black, hemispherical, 80–180 \times 190–380 μm ; columellae cylindric–campanulate to narrowly conical, 120–225 \times 120–230 μm , 60–140 μm diam. in the upper portion; sporangiospores oblong–ellipsoid, orange–yellow, 9.9–19.7 \times 5.5–9.5 μm . Zygospores not found.

NUMBER OF STRAINS STUDIED: 48.

SUBSTRATA: On dung of camels, cows, deers, dogs, donkeys, foxes, horses, monkeys, pigs, rabbits, sheep, and other animals.

DISTRIBUTION IN CHINA: Beijing; Fujian; Fuzhou, Xiamen; Guangdong; Guangzhou; Guangxi; Nanning; Guizhou; Guiyang; Hebei; Guyuan, Jixian; Hunan; Changsha; Jiangsu; Shanghai; Shaanxi; Taibaishan; Sichuan; Peiling; Xinjiang; Baerluke.

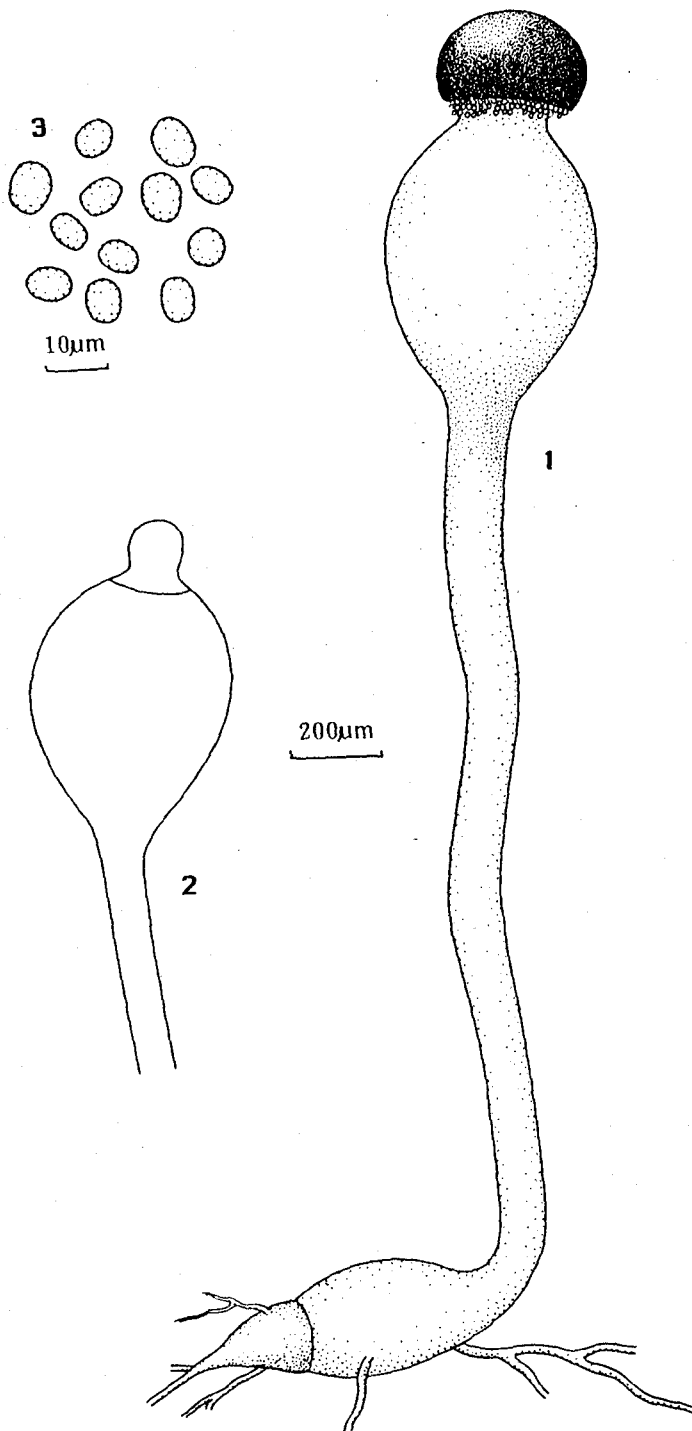


Fig. 2 *Pilobolus crystallinus* var. *hyalosporus*. 1. A fructification showing sporangium, subsporangial swelling, sporangiophore, and trophocyst. 2. A subsporangial swelling with a columella. 3. Spores. (Strain P21)

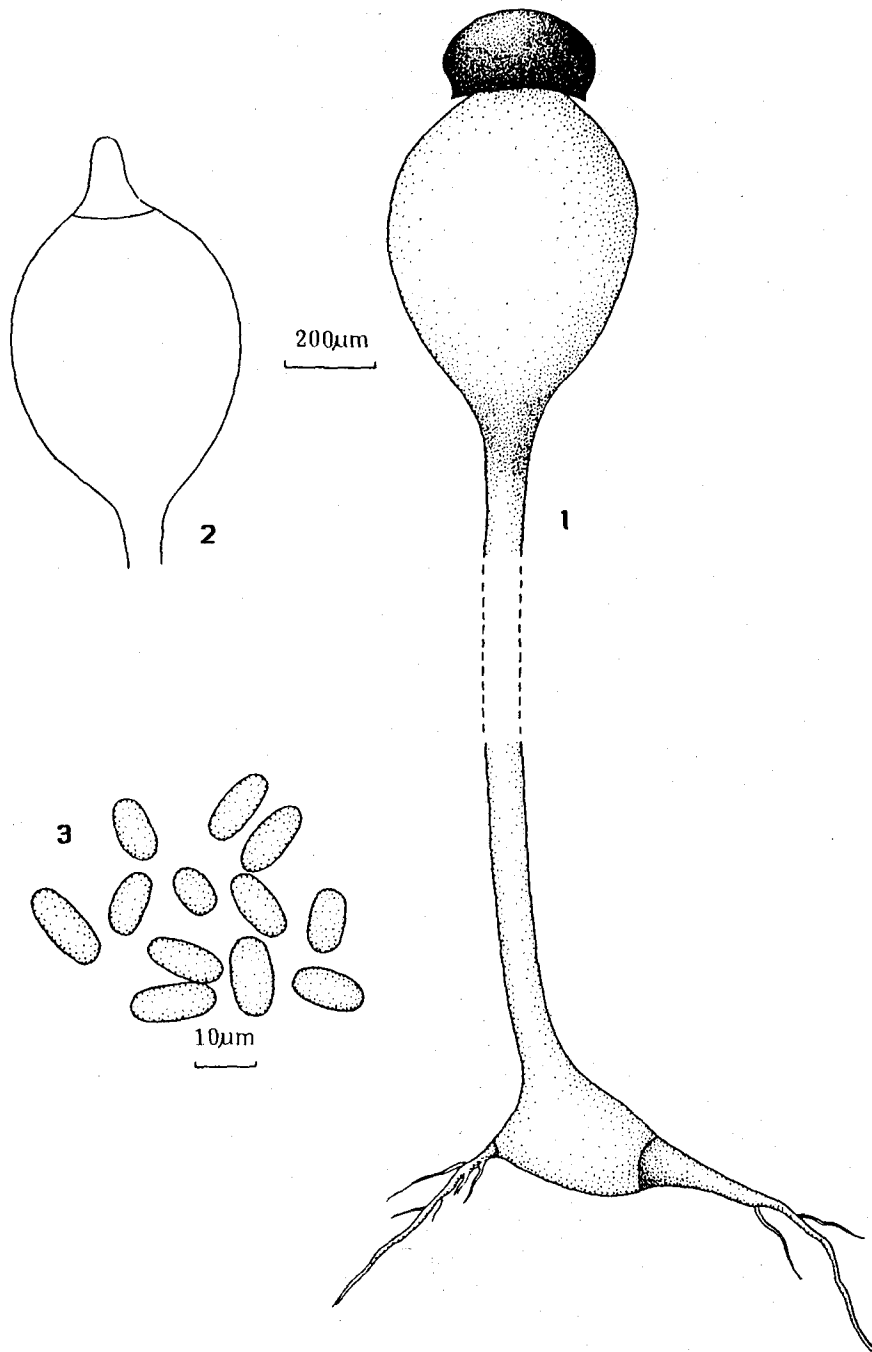


Fig. 3 *Pilobolus crystallinus* var. *kleinii*. 1. A fructification showing sporangium, subsporangial swelling, sporangiophore, and trophocyst. 2. A subsporangial swelling with a columella. 3. Spores. (Strain P2)

2-1. *Pilobolus lentiger* Corda, Icon. Fung. 1:22. 1837. var. *lentiger* (Fig. 4)

- = *Pycnopodium lentiger* (Corda) Corda, Icon. Fung. 5:18. 1842.
- = *Pilobolus exiguus* Bain., Etude Mucor., 47. 1882.
- = *Pilobolus kleinii* forma *sphaerosporus* Grove, J. Bot. 22:132. 1884.
- = *Pilobolus lentiger* var. *macrosporus* Berl. & de Toni in Sacc., Syll. Fung. 7:188. 1888.
- = *Pilobolus kleinii* var. *sphaerosporus* (Grove) Fisch. in Rabenh., Kryptogamen Flora I. 6:263. 1892.
- = *Pilobolus sphaerosporus* (Grove) Palla, Oesterr. Bot. Zeit. 50:365. 1900.
- = *Pilobolus borzianus* Morini, Mem. Accad. Sci. Ist. Bologna VI. 3:386. 1906.
- = *Pilobolus borzianus* var. *geminatus* Morini, Mem. Accad. Sci. Ist. Bologna VI. 6:225. 1909.
- = *Pilobolus kleinii* var. *sphaerosporus* (Grove) Naumov, Flora Grib. Leningr. Oblast. 1:158. 1954.

Fructifications 1–3 mm high; sporangiophores arising from the trophocysts, erect, unbranched, nonseptate, 75–130 μm diam. in the upper portion and 50–85 μm diam. in the lower portion; trophocysts ovate, buried in the substratum, 180–315 \times 115–250 μm ; subsporangial swellings obovoid to subglobose, orange–yellow at the base, 295–495 \times 225–470 μm ; sporangia black, hemispherical, 95–245 \times 165–310 μm ; columellae obtusely conical, 135–185 \times 155–210 μm ; sporangiospores globose, orange–yellow, 8–18.5 μm diam. Zygospores not found.

NUMBER OF STRAINS STUDIED: 39.

SUBSTRATA: On dung of bears, camels, cats, chickens, cows, deers, elephants, foxes, horses, leopards, monkeys, mice, mules, pandas, pigs, sheep.

DISTRIBUTION IN CHINA: Beijing; Guangdong; Guangzhou; Shandong; Qingdao; Shanxi; Yongji; Yunnan; Kunming.

2-2. *Pilobolus lentiger* var. *minutus* (Speg.) Zheng & G.–q. Chen comb. nov. (Fig. 5)

- = *Pilobolus minutus* Speg., Anal. Soc. Cient. Argent. 9:176. 1880.
- = *Pilobolus kleinii* var. *minor* Dewèvre, Grevillea 22:78. 1894.
- = *Pilobolus morinii* Sacc., Syll. Fung. 17:505. 1905.

Fructifications 2.5–4.5 mm high; sporangiophores arising from the trophocysts, erect, unbranched, nonseptate, 70–115 μm diam. in the upper portion, 55–90 μm diam. in the lower portion; trophocysts subglobose or ovoid, buried in the substratum, 245–415 \times 185–275 μm ; subsporangial swellings obovoid to subglobose, orange–yellow at the base, 330–655 \times 255–520 μm ; sporangia black, hemispherical, 110–200 \times 220–335 μm ; columellae obtusely and broadly cylindrical to narrowly conical, 120–215 μm high, 110–215 μm diam. in the upper portion and 145–200 μm diam. in the lower portion; sporangiospores globose to subglobose, usually deep yellow, sometimes lighter, (4.8–)5.4–6.9(–8.6) μm diam. Zygospores not found.

NUMBER OF STRAINS STUDIED: 4.

SUBSTRATA: On dung of camels, donkeys, mules, and sheep.

DISTRIBUTION IN CHINA: Beijing; Guangdong; Guangzhou.

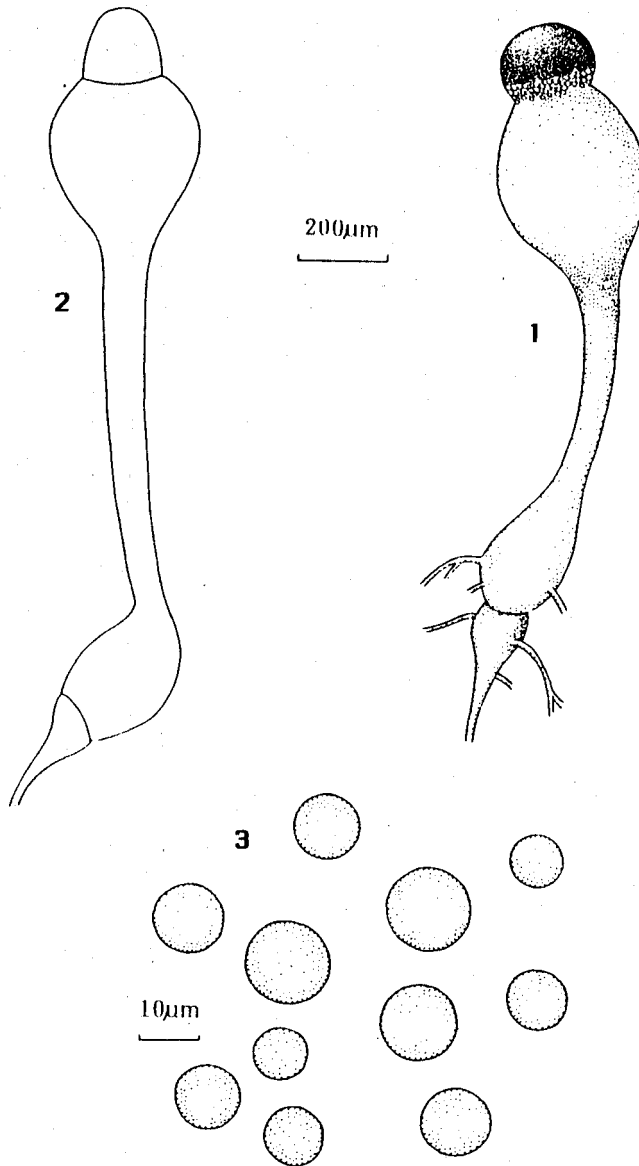


Fig. 4 *Pilobolus lentiger* var. *lentiger*. 1. A fructification showing sporangium, subsporangial swelling, sporangiophore, and trophocyst. 2. A subsporangial swelling with a columella. 3. Spores. (Strain P1)

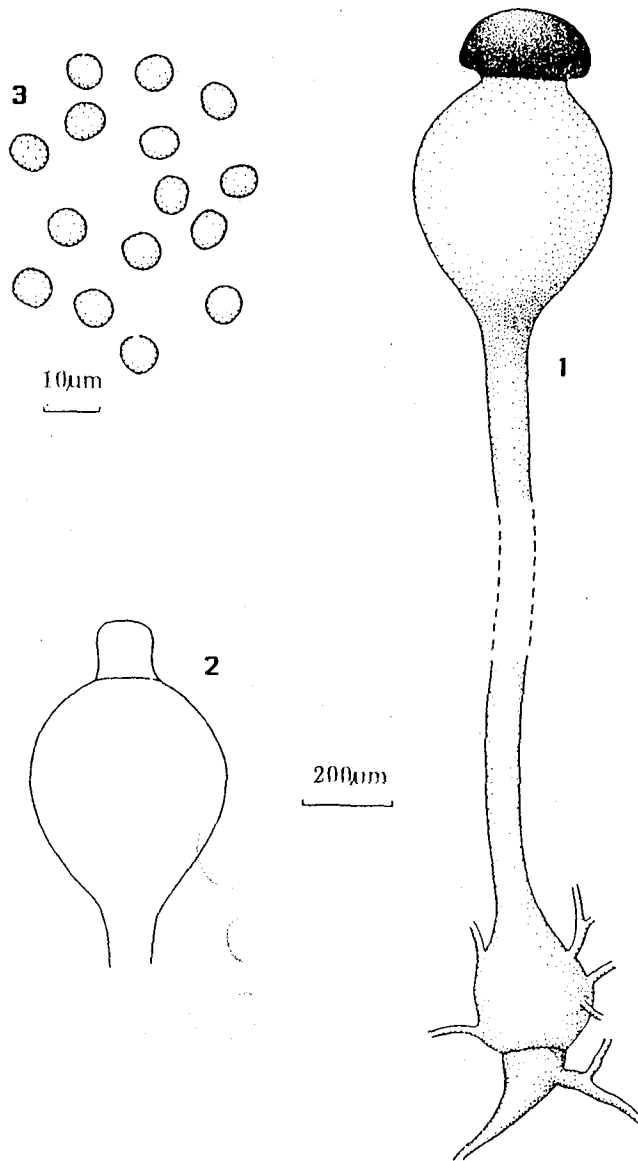


Fig. 5 *Pilobolus lentiger* var. *minutus*. 1. A fructification showing sporangium, subsporangial swelling, sporangiophore, and trophocyst. 2. A subsporangial swelling with a columella. 3. Spores. (Strain P26)

3. *Pilobolus longipes* van Tieghem, Ann. Sci. Nat. Bot., Ser. VI. 4:338. 1876. (Fig. 6)

Fructifications 11–35 mm high; sporangiophores arising from the trophocysts, erect, unbranched, nonseptate, usually perpendicular to the trophocysts, 145–220 μm diam. in the upper portion, 80–170 μm diam. in the lower portion; trophocysts elongate, very long, yellow, external and parallel to the substratum, 465–1730 \times 220–690 μm ; subsporangial swellings obovoid, light orange, 510–1200 \times 395–870 μm ; sporangia black, hemispherical, 150–435 \times 255–515 μm ; columellae obtusely conical to obtusely and broadly cylindrical, 170–340 \times 320–435 μm , 180–340 μm diam. in the upper portion; sporangiospores broadly ovoid to subglobose, yellowish–orange, 8.7–13.6 \times 7.4–12.4 μm , thick-walled. Zygospores not found.

NUMBER OF STRAINS STUDIED: 17.

SUBSTRATA: On dung of camels, cows, elephants, horses, mules, and sheep.

DISTRIBUTION IN CHINA: Beijing; Guangxi; Nanning; Guizhou; Guiyang; Hebei; Guyuan; Jiangsu; Yangzhou, Zhenjiang; Ningxia; Yinchuan.

4. *Pilobolus oedipus* Mont., Mém. Soc. Linn. Lyon; 1. 1836. (Fig. 7)

= *Pilobolus reticulatus* van Tieghem, Ann. Sci. Nat. Bot., Ser. VI. 4:336. 1876.

= *Pilobolus argentinus* Speg., Anal. Soc. Cient. Argent. 9:176. 1880.

Fructifications 1.5–5 mm high; sporangiophores arising from the trophocysts, erect, unbranched, nonseptate, 95–160 μm diam.; trophocysts subglobose or napiform, dirty yellow, buried in the substratum, 305–410 \times 270–360 μm ; subsporangial swellings obovoid, 430–620 \times 365–545 μm ; sporangia black, hemispherical, 180–225 \times 280–495 μm ; sporangiospores broadly ovoid to globose, orange yellow, 11.2–13.6 \times 9.9–11.2 μm or 9.9–11.2 μm diam., with a very thick wall which is about 1.2 μm wide and deep brown. Zygospores not found.

NUMBER OF STRAINS STUDIED: 2.

SUBSTRATUM: On horse dung.

DISTRIBUTION IN CHINA: Guangdong; Guangzhou; Guangxi; Nanning.

5-1. *Pilobolus roridus* (Bolt.:Fr.) Pers., Syn. Meth. Fung.:118. 1801. var. **roridus** (Fig. 8)

= *Mucor roridus* Bolt.:Fr., Hist. Fung. 3:168. 1789.

= *Pilobolus microsporus* Klein, Verh. Zool.-Bot. Ges. Wien 20:556. 1870.

= *Pilobolus crystallinus* subsp. *anisosporus* Lyr, Arch. Protist. 99:261. 1954. nom. illegit. (not validly published)

= *Pilobolus crystallinus* subsp. *typicus* Lyr, Arch. Protist. 99:260. 1954. nom. illegit. (not validly published)

Fructifications 4–12 mm high; sporangiophores arising from the trophocysts, erect, unbranched, nonseptate, 60–125 μm diam. in the upper portion, 45–80 μm diam. in the lower portion; trophocysts ovate–cylindric, buried in the substratum, 210–345 \times 120–285 μm ; subsporangial swellings ovoid to elliptic–ovoid, orange yellow at the base, 450–885 \times

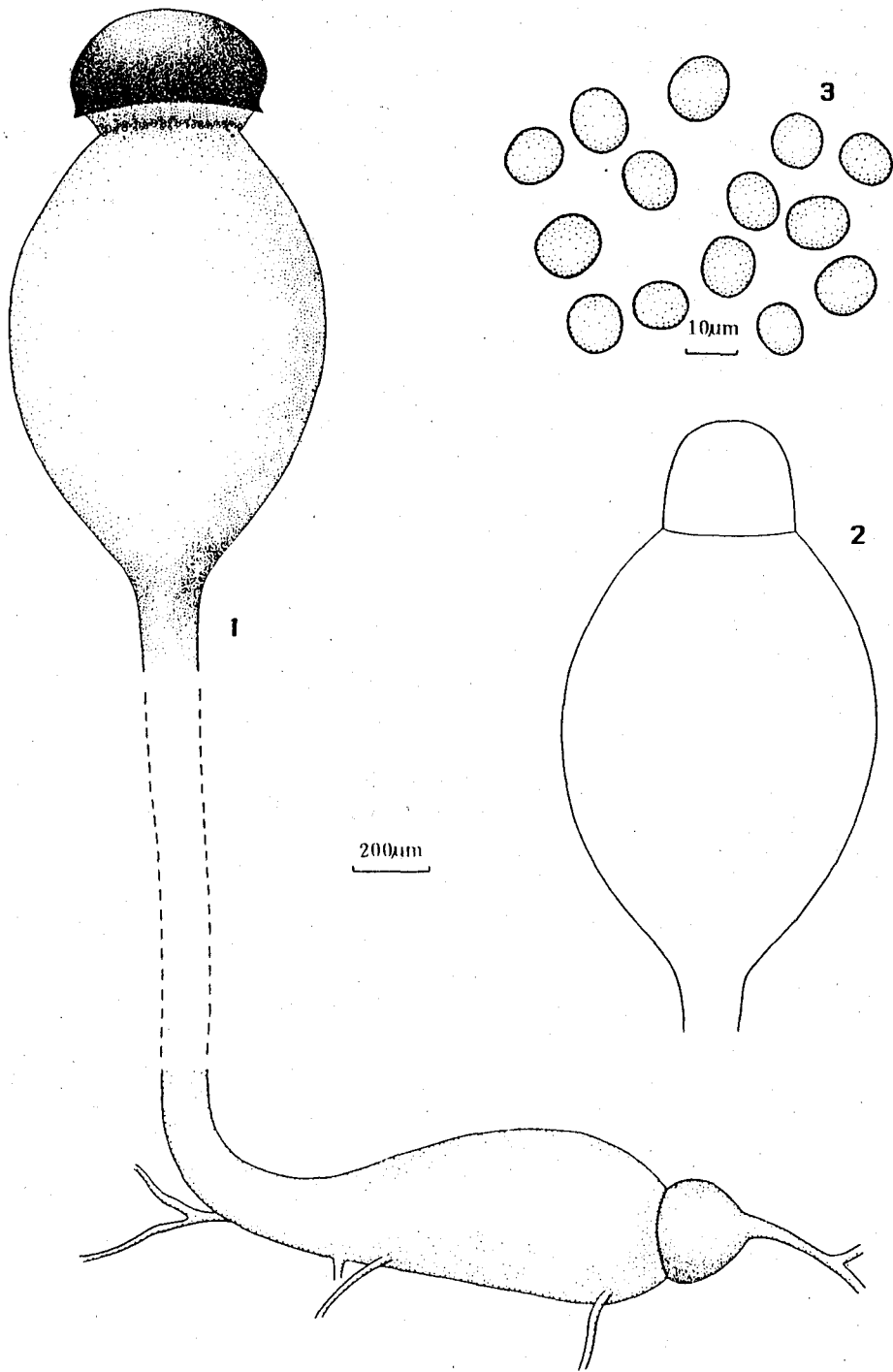


Fig. 6 *Pilobolus longipes*. 1. A fructification showing sporangium, subsporangial swelling, sporangiophore, and trophocyst. 2. A subsporangial swelling with a columella. 3. Spores. (Strain P12)

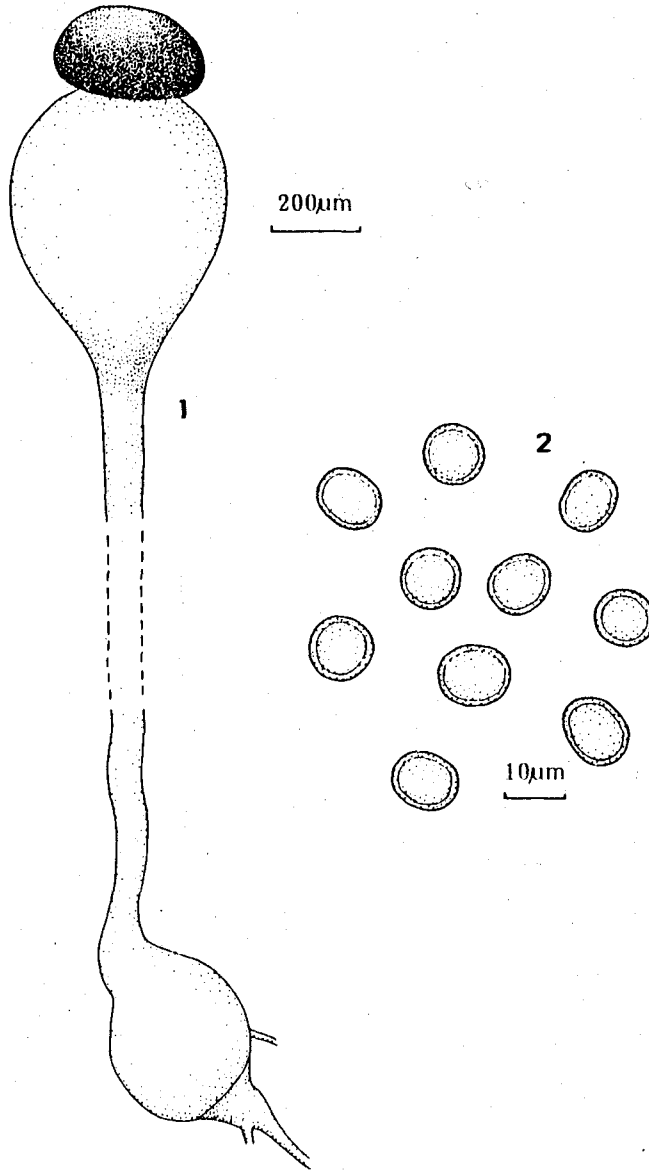


Fig. 7 *Pilobolus oedipus*. 1. A fructification showing sporangium, subsporangial swelling, sporangiophore, and trophocyst. 2. Spores. (Strain P163)

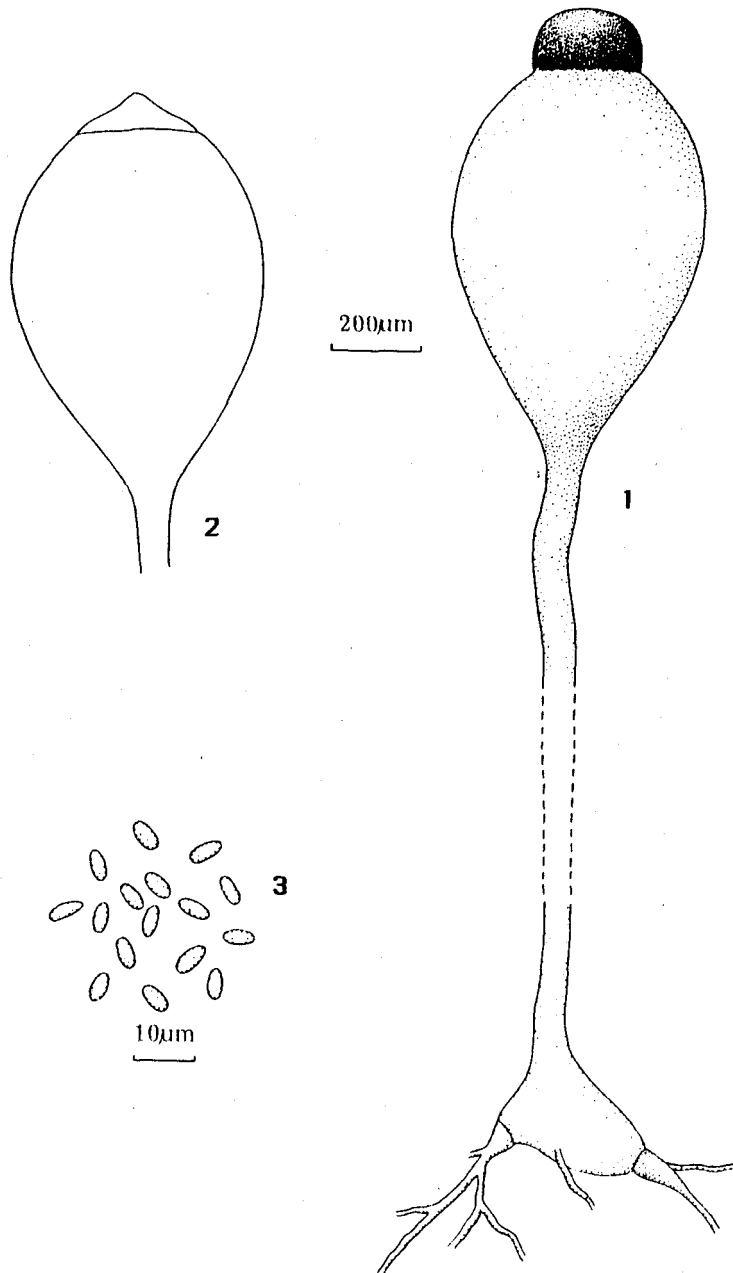


Fig. 8 *Pilobolus roridus* var. *roridus*. 1. A fructification showing sporangium, subsporangial swelling, sporangiophore, and trophocyst. 2. A subsporangial swelling with a columella. 3. Spores. (Strain P27)

380–555 μm ; sporangia black, hemispherical, 110–140 \times 145–330 μm ; columellae plano-convex, somewhat greyish, 65–80 \times 220–330 μm ; sporangiospores oblong-ellipsoid, light yellow to subhyaline, 4.5–7 \times 3–4.5 μm . Zygospores not found.

NUMBER OF STRAINS STUDIED: 28.

SUBSTRATA: On dung of camels, chickens, cows, pigs, sheep, and other animals.

DISTRIBUTION IN CHINA: Beijing; Guangdong; Guangzhou; Guizhou; Tongren; Jiangsu; Nanjing; Shaanxi; Taibaishan; Shandong; Qingdao; Shanxi; Yongji; Sichuan; Chengdu, Wulong; Yunnan; Kunming.

5-2. *Pilobolus roridus* var. *umbonatus* (Buller) Hu & Zheng comb. nov. (Fig. 9)

= *Pilobolus umbonatus* Buller, Researches on Fungi 6:178. 1934.

Fructifications 3–10 mm high; sporangiophores arising from the trophocysts, erect, unbranched, nonseptate, 80–105 μm diam. in the upper portion, 50–75 μm diam. in the lower portion; trophocysts ovate to turbinate, buried in the substratum, 210–360 \times 145–260 μm ; subsporangial swellings ovoid to elliptic-ovoid, orange yellow at the base, 455–745 \times 380–535 μm ; sporangia black, hemispherical and umbonate, 85–160 \times 170–290 μm ; columellae plano-convex, somewhat greyish, 55–115 \times 185–275 μm ; sporangiospores oblong-ellipsoid, light yellow to subhyaline, 5.3–7.4 \times 3–3.8 μm . Zygospores not found.

NUMBER OF STRAINS STUDIED: 13.

SUBSTRATA: On dung of camels, cows, pigs, sheep, and other animals.

DISTRIBUTION IN CHINA: Beijing; Guangdong; Guangzhou; Guizhou; Tongren; Jiangsu; Nanjing; Shaanxi; Taibaishan; Shandong; Qingdao; Shanxi; Yongji; Sichuan; Wulong; Yunnan; Kunming.

DOUBTFUL SPECIES

1. *Mucor obliquus* Scop., Flora Carniol. 2:494. 1772.
2. *Mucor urceolatus* Dicks., Fasc. Plant Crypt. 1:25. 1785.
3. *Pilobolus urceolatus* Purt., Midland Flora 3:323. 1821.
4. *Pilobolus pestis-bovinae* Hallier, Zeitschr. Parasitenk. p. 57. 1872.
= *Pilobolus hallierii* Rivolta, Paras. Veget. ed. II. p. 497. 1884.
5. *Pilobolus nanus* van Tieghem, Ann. Sci. Nat. Bot., Ser. VI. 4:340. 1876.
6. *Pilobolus intermedius* (Coem.) P. A. Karsten, Bidr. Kann. Finlands Nat. Folk 31:71. 1879.
= *Pilobolus oedipus* var. *intermedius* Coem., Bull. Acad. Belg. II. 16:71. 1863.
7. *Pilobolus pullus* Masee, Kew Bull. 175–177:160. 1901.
8. *Pilobolus proliferens* McVickar, Amer. J. Bot. 29:378. 1942.
9. *Pilobolus ramosus* McVickar, Amer. J. Bot. 29:379. 1942.
10. *Pilobolus simplex* McVickar, Amer. J. Bot. 29:379. 1942.
11. *Pilobolus lentiger* forma *kleinii* Reyn. & Laysa, Philipp. Agric. 50:780. 1967.
12. *Pilobolus lentiger* forma *minutus* Reyn. & Laysa, Philipp. Agric. 50:780. 1967.

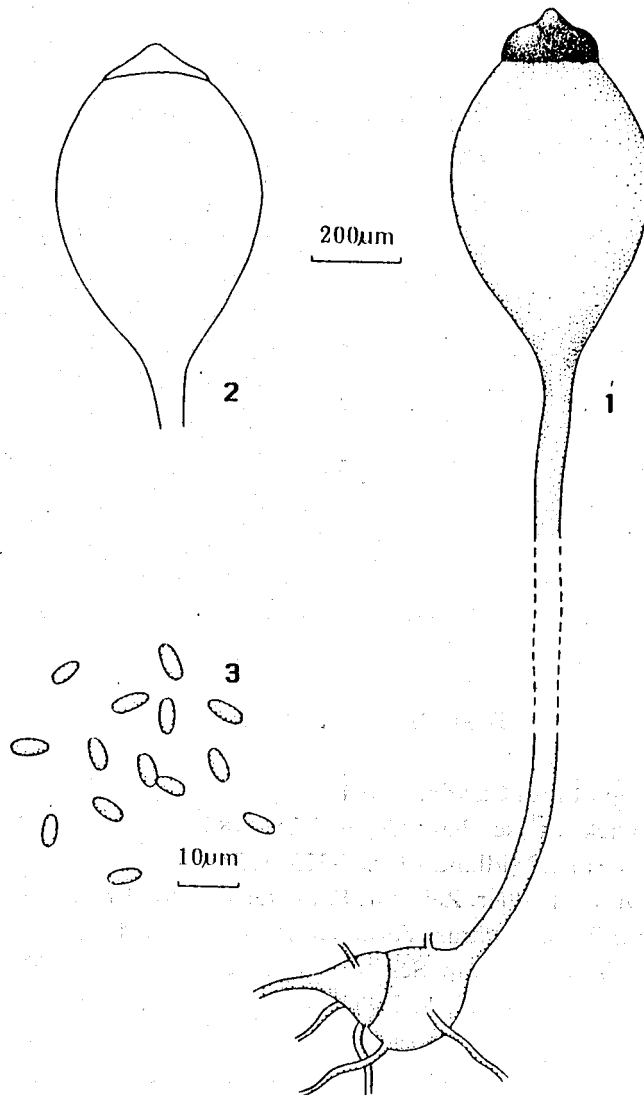


Fig. 9 *Pilobolus roridus* var. *umbonatus*. 1. A fructification showing sporangium, subsporangial swelling, sporangiophore, and trophocyst. 2. A subsporangial swelling with a columella. 3. Spores. (Strain P73)

ACKNOWLEDGEMENTS

We are very grateful to Drs. R. K. Benjamin and P. M. Kirk for their valuable suggestions and critical review of the paper. We thank Dr. R. P. Korf for checking some of the literature problems. We also thank Ms Han Zhe-fang for inking the line drawings.

REFERENCES

- Benjamin CR, Hesseltine CW (1959) Studies on the genus *Phycomyces*. *Mycologia* **50**:751-771
- Benjamin RK (1979) Zygomycetes and their spores. pp 573-616. In: Kendrick WB (ed) *The Whole Fungus*. National Museum of Canada, Ottawa
- Benny GL (1982) Zygomycetes. pp 184-195. In: Parker SP (ed) *Synopsis and Classification of Living Organisms*. Vol I. McGraw-Hill, New York
- Boedijn KB (1958) Notes on the Mucorales of Indonesia. *Sydowia* **12**:321-362
- Brefeld O (1881) *Chaetocladium*, *Pilobolus*, *Mortierella*. *Unters Gesgeb Mykol* **4**:1-191
- Cohn F (1851) Die Entwicklungsgeschichte des *Pilobolus crystallinus*. *Nova Acta Acad Caes L-C Nat Cur* **23**:493-535
- Corda ACJ (1837) *Icones Fungorum* **1**:1-32
- Dewèvre A (1894) Contribution a l'Etude des Mucorinées; Pilobolées. *Grevillea* **22**:69-79
- Fang XF (1941) Two species of Mucorales on pig dung found in Wutungkiao. *Huanghai* **2**:159-160 (in Chinese)
- Fang XF (1942) Identification of some Mucorales in Sichuan Province. *Huanghai* **3**:165-170 (in Chinese)
- Fischer A (1892) Phycomycetes: Mucorinae. In: Rabenhorst L, *Kryptogamenflora von Deutschland, Oesterreich und der Schweiz* I. **4**:161-310
- Ginai MA (1936) Further contribution to a knowledge of Indian coprophilous fungi. *J Indian Bot Soc* **15**:269-284
- Gronvold J, Jorgensen RJ (1987) Spread of lungworm (*Dictyocaulus viviparus*) infection by *Pilobolus* fungi among stabled calves. *Prev Vet Med* **5**:43-50
- Grove WB (1934) A systematic account and arrangement of the Pilobolidae. pp 190-224. In: Buller AHR, *Researches on Fungi* Vol 6. Hafner Pub Co, New York
- Hesseltine CW (1950) A revision of the Mucorales based especially upon a study of the representatives of this order in Wisconsin. Thesis pp 1-1570
- Hesseltine CW (1952) A survey of the Mucorales. *Trans New York Acad Sci* **14**:210-214
- Hesseltine CW, Ellis JJ (1973) Mucorales. pp 187-217. In: Ainsworth GC, Sparrow FK, Sussman AS (eds) *The Fungi* Vol IVB. Academic Press, New York
- Kirk PM, Benny GL (1980) The genus *Utharomyces* Boedijn (Pilobolaceae; Zygomycetes). *Trans Brit Mycol Soc* **75**:123-131
- Lendner A (1908) Les Mucorinées de la Suisse. Beiträge zur Kryptogamenflora der Schweiz III. **1**:1-180
- McVickar DL (1942) The light controlled diurnal rhythm of asexual reproduction in *Pilobolus*. *Amer J Bot* **29**:372-380
- Mikawa T (1979) A taxonomic study on Japanese sporangiferous Mucorales (5). *J Japan Bot* **54**(7):193-203
- Milko AA (1974) Opredelitel Mukoralnyk Gribov. Akad Nauk Ukrain SSR Kiev. pp 1-303 (in Russian)

- Nand K, Mehrotra BS (1968) Species of *Pilobolus* and *Pilaira* from India. *Sydowia* **22**:299-306
- Nand K, Mehrotra BS (1977) Species of *Pilobolus* and *Pilaira* from India. *Sydowia* **30**:283-289
- Naumov NA (1939) Clés des Mucorinées (Mucorales). *Encycl Mycol* **9**:1-137
- Naumov NA (1954) Poryadok Mucorales. Flora Grib Leningr Oblast **1**:118-168 (in Russian)
- Ou SH (1940) Phycomycetes of China I. *Sinensia* **11**:33-57
- Reynolds DR, Laysa FND (1967) Notes on Philippine *Pilobolus*. *Philipp Agric* **50**: 779-783
- Spegazzini C (1880) Fungi Argentini, pugillus primus. *Anal Soc Cient Argent* **9**: 158-192
- Tai FL (1979) Sylloge Fungorum Sinicorum. Science Press, Beijing. pp 1-1527 (in Chinese)
- von Arx JA (1982) On Mucoraceae s. str. and other families of the Mucorales. *Sydowia* **35**:10-26
- Zheng RY, Hu FM (1979) Mucorales of China. In: Tai FL, Sylloge Fungorum Sinicorum. Science Press, Beijing. pp 1-1527 (in Chinese)
- Zycha H (1935) Mucorineae. In: Rabenhorst L, Kryptogamenflora der Mark Brandenburg VIa:1-264
- Zycha H, Siepman R, Linnemann G (1969) Mucorales. Cramer, Lehre. pp 1-355

水玉霉 (*Pilobolus*) 属的种的新划分

胡复眉 郑儒永 陈桂清

中国科学院微生物研究所

真菌地衣系统学开放研究实验室

北京

摘要: 我们在过去的工作中承认水玉霉(*Pilobolus*)属的9个种(郑、胡, 见戴, 1979)。近年来我们重新分离得到了这些分类群并对它们进行了再研究。研究表明, 尽管它们是彼此可以互相区分的分类群, 但是, 包括我们过去的概念在内, 目前被普遍接受的用于这个属的分类的种概念太小。为了与整个毛霉目的其它属的分类系统相一致, 我们把这9个分类群重新划分为由9个变种组成的5个种: 晶澈水玉霉原变种 [*Pilobolus crystallinus* (Wigg.) Tode var. *crystallinus*], 晶澈水玉霉透孢变种新组合 [*P. crystallinus* var. *hyalosporus* (Boedijn) Hu & Zheng, comb. nov.], 晶澈水玉霉克莱因变种新组合 [*P. crystallinus* var. *kleinii* (van Tieghem) Zheng & G.-q. Chen, comb. nov.], 豆状水玉霉原变种 (*P. lentiger* Corda var. *lentiger*), 豆状水玉霉小型变种新组合 [*P. lentiger* var. *minutus* (Speg.) Zheng & G.-q. Chen, comb. nov.], 长型水玉霉 (*P. longipes* van Tieghem), 厚壁水玉霉 (*P. oedipus* Mont.), 露水玉霉原变种 [*P. roridus* (Bolt.) Pers. var. *roridus*], 露水玉霉突囊变种新组合 [*P. roridus* var. *umbonatus* (Buller) Hu & Zheng, comb. nov.]. 水玉霉属先后报道过的种或种下分类群名称共计50个左右, 其中一些异名往往被不同的作者归到不同的正名下面。为了解决它们的正确归属问题, 我们对全部原始描述作了细致的文献考证然后决定其位置。对那些找不到原始描述或从原始描述中得不出结论的则作为可疑名称处理。可疑名称共计12个: *Mucor obliquus* Scop., *M. urceolatus* Dicks., *Pilobolus urceolatus* Purt., *P. pestis-bovinae* Hallier (= *P. hallierii* Rivolta), *P. nanus* van Tieghem, *P. intermedius*

(Coem.) P. A. Karsten (= *P. oedipus* Mont. var. *intermedius* Coem.), *P. pullus* Masee, *P. proliferens* McVickar, *P. ramosus* McVickar, *P. simplex* McVickar, *P. lentiger* forma *kleinii* Reyn. & Laysa, *P. lentiger* forma *minutus* Reyn. & Laysa. 水玉霉属内的种和变种可区分如下:

水玉霉属分种和变种检索表

- 1. 孢子椭圆形, 长度不超过 $7\mu\text{m}$; 囊轴扁平凸镜形, 高度不超过 $110\mu\text{m}$ 2
- 1. 孢子不是椭圆形, 如椭圆形则长度超过 $7\mu\text{m}$; 囊轴不是扁平凸镜形, 高度一般超过 $110\mu\text{m}$ 3
- 2. 孢子囊不作乳突状 5-1. 露水玉霉原变种
- 2. 孢子囊乳突状 5-2. 露水玉霉突囊变种
- 3. 孢子椭圆形且长度超过 $7\mu\text{m}$ 或广卵形; 囊轴狭窄钟状; 子实体中型[高度 2-12(-14) mm] 4
- 3. 孢子近球形至球形; 囊轴圆锥形, 中部不缢缩; 子实体大型(高度 11-35mm) 或小型(高度 1-5mm) 6
- 4. 孢子 $7-10 \times 4.5-6\mu\text{m}$ 1-1. 晶澈水玉霉原变种
- 4. 孢子较长或较宽 5
- 5. 孢子 $6.5-9.5 \times 5.5-8.5\mu\text{m}$, 无色, 至多淡黄色 1-2. 晶澈水玉霉透孢变种
- 5. 孢子 $10-20 \times 5.5-9.5\mu\text{m}$, 深黄色 1-3. 晶澈水玉霉克莱因变种
- 6. 子实体大型; 营养囊在基物外形成, 很长, 长度可达 $1730\mu\text{m}$ 3. 长型水玉霉
- 6. 子实体小型; 营养囊在基物内形成, 不长, 长度一般不超过 $500\mu\text{m}$ 7
- 7. 孢子厚壁, 广卵形, 近球形至球形 4. 厚壁水玉霉
- 7. 孢子薄壁, 球形 8
- 8. 孢子直径 $8-18.5\mu\text{m}$ 3-1. 豆状水玉霉原变种
- 8. 孢子直径 $5.5-7(-8.5)\mu\text{m}$ 3-2. 豆状水玉霉小型变种

关键词: 水玉霉属; 水玉霉科; 毛霉目; 真菌; 分类