A monograph of Rhizopus

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A total of 312 *Rhizopus* strains comprising 187 strains isolated in China and 125 strains from foreign countries have been studied, which include possibly all of the cultures derived from types available now. The morphology of the sporangial and zygosporic states, maximum growth temperature, mating compatibility, and molecular systematics were used as important reference for the classification of the genus. Seventeen taxa, ten species and seven varieties, are recognized in the genus *Rhizopus* in this study. These include: *R. americanus, R. arrhizus* var. *arrhizus, R. arrhizus* var. *delemar, R. arrhizus* var. *tonkinensis, R. caespitosus, R. homothallicus, R. microsporus* var. *microsporus, R. microsporus* var. *azygosporus, R. microsporus* var. *chinensis, R. microsporus* var. *oligosporus, R. microsporus* var. *rhizopodiformis, R. microsporus* var. *tuberosus, R. niveus, R. reflexus, R. schipperae, R. sexualis,* and *R. stolonifer*. Seventy-two names of *Rhizopus* are treated as synonyms. Twenty-five species, eight varieties and one form are thought to be doubtful, and nine species and four varieties are excluded from the genus. Neotypes are designated for *R. microsporus* var. *microsporus, R. microsporus* var. *oligosporus, R. microsporus* var. *rhizopodiformis,* and *R. stolonifer*. In the taxa accepted, zygospores are found and studied in all the three homothallic species and five heterothallic species or varieties; while azygospores are found in two species and one variety. A synoptic key and a diagnostic key, as well as synonyms, descriptions, and line drawings are provided for all taxa recognized.

Key words: Mucorales, Zygomycota, taxonomy, morphology, holomorph.

Members of the genus *Rhizopus* are closely related to mankind in many aspects. Industrially, they are important fermentation agents, especially in food industry. Agriculturally, they cause decay of plant products in transit and storage, and, under favorable conditions, they cause diseases in plants. Medically, they are known as producers of medicines or they catalyze the formation of such drugs, and are found to be more and more important in causing mucormycosis in man and animals.

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Owing to their economic importance, many *Rhizopus* strains were found and isolated from artificial environments of production practice quite different to natural habitats. These strains have undergone many generations and already adapted themselves to such conditions. One of the important changes is their morphology which makes their identification and classification very difficult. Taxonomists working on *Rhizopus* may have the experience that *R. stolonifer* and its allies (equivalent to the *R. stolonifer* Group of Schipper 1984) are easier to classify than *R. microsporus* and its allies (equivalent to the *R. microsporus* Group of Schipper & Stalpers 1984), and, the most difficult ones, *R. arrhizus* and its allies (equivalent to the species *R. oryzae* of Schipper 1984). This is because that most strains of *R. stolonifer* and its allies are from nature and capable of retaining their natural morphology; the situation of *R. microsporus* and its allies is intermediate – part of the taxa are from nature and part of the taxa are from artificial environments; while most strains of *R. arrhizus* and its allies are no more "natural species" but long-term fermentative agents which have already changed vigorously in their morphology. Nevertheless, if the morphology, developed through long-term adaptation to the fermentation environment, is stable enough for recognition, the species is accepted in this study.

Like in other genera of the Mucorales, the taxonomy of *Rhizopus* is based primarily on morphology. Only a few authors classified species by strict morphology (Fischer 1892, Yamamoto 1930, Naumov 1939). In early works, physiological characteristics were also used as important criteria. The most universal characteristic that has been used and lasted till recently is growth temperature, especially maximum growth temperature (Lendner 1908, Hagem 1910, Hanzawa 1912 and 1915, Yamazaki 1934, Zycha 1935, Zycha *et al.* 1969, Kocková-Kratochvilová & Palkoska 1958, Schipper 1984, Schipper & Stalpers 1984). Physiological characteristics other than temperature include: fermentation of sugars (Lendner 1908, Hanzawa 1912) and formation of acids (Takahashi & Sakaguchi 1925 and 1926). Since then, formation of acids was seldom used to classify species until Abe *et al.* (2003) claimed that organic acid patterns can be used as a systematic criterion for *Rhizopus* taxa because a clear relationship between rDNA-ITS sequences and organic acid production exists, and that ITS sequencing is an effective and simpler method for classification. After a thorough and comprehensive study of all the reported morphological, cultural and physiological characteristics of 449 strains, Inui *et al.* (1965) came to the conclusion that only the following 10 characters are of prime importance to the classification of *Rhizopus:* (1) maximum growth termperature, (2) formation of chlamydospores, (3) formation of sporangia and rhi-

zoids, (4) curvature of sporangiophores, (5) colour of sporangiophores, (6) diameter of sporangia, (7) colour of the reverse side of mycelial mat on liquid cultural media containing sodium glutamate, (8) acid produced by surface culture, (9) Voges-Proskauer test, and (10) shape and size of sporangiospores. In later works, more criteria have been adopted to distinguish some of the controversial species, for example, spore ornamentation by SEM (D. H. Ellis 1981, Seviour *et al.* 1983, Liou *et al.* 1991), electrophoretic patterns of sporangiospore proteins (Seviour *et al.* 1985) or mycelial proteins (Liou *et al.* 2001), serological test (Polonelli *et al.* 1988), DNA complementarity (Ellis 1985, 1986), mol% G+C (Frye & Reinhardt 1993), numerical taxonomy (Dabinett & Wellman 1973), and computer coding (Jong & McManus 1993).

In this laboratory, a synthetic study on the following four aspects: morphology of the sporangial and zygosporic states, maximum growth temperature, mating compatibility and zygospore formation, and molecular systematics has been investigated in order to solve problems encountered in the taxonomy of *Rhizopus*. Because the paper presented here is already very voluminous, results of molecular systematics will be published in one or two separate papers later on. One hundred and thirty-six names have been introduced in this genus. Table 1 summarizes the status of names published by previous taxonomies as well as our treatments in the present study.

A total of 312 strains comprising 187 strains isolated in China and 125 strains from foreign countries have been studied and classified into ten species and seven varieties; this material possibly includes all of the cultures derived from types available now.

Materials and Methods

Cultures

Details of materials studied are presented under the description of each taxon. Strains were obtained from American Type Culture Collection, Virginia, USA (ATCC), Centraalbureau voor Schimmelcultures, Utrecht, Netherlands (CBS), Faculty of Engineering, Hiroshima University, Japan (HUT), the Institute for Fermentation, Osaka, Japan (IFO), Japan Collection of Microorganisms, Riken, Japan (JCM), and the USDA Agricultural Research Service Collection, Peoria, USA (NRRL); those from China were isolated and identified by us and maintained in the Culture Collection of the Key Laboratory of Systematic Mycology & Lichenology (with a 'R-' prefix for *Rhizopus* spp.) or the AS Culture Collection (with acronym AS), both of the Institute of Microbiology, Chinese Academy of Sci-

Table 1. Treatments of *Rhizopus* taxa by different authors.

Rhizopus	Lendner 1908	Hanzawa 1915	Yamamoto 1930	Naumov 1939	Kocková-Kratochvílová & Palkoska 1958	Inui *et al.* 1965	Zycha *et al.* 1969	Pidoplichko & Milko 1971	Milko 1974	Schipper 1984	Schipper & Stalpers 1984	Ellis 1985	Ellis 1986	Zheng *et al.* this study
1) *R. acetoinus*	—	—	—	—	—	—	—	—	93	—	—	—	—	9
2) *R. achlamydosporus*	—	—	—	—	—	46	93	—	39	93	—	—	—	10
3) *R. acidus*	—	—	93	—	—	39	—	93	93	—	—	—	—	10
4) *R. albus*	—	—	✓	—	—	—	—	—	93	—	—	—	—	9
5) *R. alpinus*	—	—	—	✓	—	—	—	38	38	—	—	—	—	75
6) *R. americanus*	—	—	—	—	—	—	—	—	—	—	—	—	—	✓
7) *R. angulisporus*	—	—	—	✓	—	—	—	39	39	—	—	—	—	**?**
8) *R. apiculatus*	—	—	—	✓	—	—	—	—	—	—	—	—	—	**?**
9) *R. arrhizus*	✓	✓	✓	✓	✓	✓	✓	93	93	**?**	—	✓	✓	✓
10) *R. arrhizus var. delemar*	—	—	—	—	—	—	—	—	—	—	—	◊	✓	✓
11) *R. arrhizus var. rouxii*	—	—	—	—	—	—	—	—	—	—	—	◊	✓	9
12) *R. arrhizus var. tonkinensis*	—	—	—	—	—	—	—	—	—	—	—	—	—	◊
13) *R. artocarpi* [Racib.]	—	—	✓	✓	—	—	81	14	14	122	—	—	—	122
14) *R. artocarpi* [(Berk .& Broome) Boedijn]	—	—	—	—	—	—	—	✓	✓	**?**	—	—	—	115
15) *R. artocarpi* var. *luxurians*	—	—	—	—	—	—	—	—	—	—	—	—	—	×
16) *R. azygosporus*	—	—	—	—	—	—	—	—	—	—	—	—	—	70
17) *R. bahrnensis*	—	—	—	—	—	—	—	—	39	93	—	—	—	10
18) *R. bankul*	—	—	—	93	—	—	—	93	93	—	—	—	—	**?**
19) *R. batatas*	—	✓	93	✓	—	93	—	57	57	93	—	—	—	9
20) *R. betavorus*	—	—	—	✓	—	—	—	93	93	—	—	—	—	×
21) *R. betivorus*	—	—	—	—	—	—	—	—	—	—	—	—	—	**?**
22) *R. biourgei*	—	—	—	—	—	—	—	—	—	—	—	—	—	**?**
23) *R. boreas*	—	—	87	—	—	57	—	—	93	93	—	—	—	12
24) *R. bovinus*	—	—	—	—	—	—	9	—	—	—	72	—	—	72
25) *R. caespitosus*	—	—	—	—	—	—	—	—	—	—	—	—	—	✓
26) *R. cambodja*	✓	—	—	✓	—	—	—	93	93	—	—	—	—	**?**
27) *R. candidus*	—	—	—	—	—	—	—	—	—	—	—	—	—	**?**
28) *R. chinensis*	✓	✓	✓	✓	—	✓	—	38	38	—	72	—	—	72
29) *R. chinensis* var. *chungyuen*	—	—	—	—	—	—	—	—	×	—	—	—	—	×
30) *R. chinensis* var. *liquifaciens*	—	—	—	—	—	—	—	—	93	—	72	—	—	75
31) *R. chinensis* var. *rugulosus*	—	—	—	—	—	—	—	—	93	—	—	—	—	72
32) *R. chiuniang*	—	—	93	—	—	39	—	—	93	—	—	—	—	10
33) *R. chiuniang* var. *isofermentarius*	—	—	—	—	—	—	—	—	—	—	—	—	—	×
34) *R. chlamydosporus*	—	—	—	—	—	—	—	69	69	—	—	—	—	9
35) *R. chungkuoensis*	—	—	93	—	—	39	—	—	93	93	—	—	—	10
36) *R. chungkuoensis* var. *isofermentarius*	—	—	—	—	—	39	—	—	93	—	—	10	—	10
37) *R. circinans*	✓	—	—	✓	✓	—	✓	—	—	**?**	—	—	—	**?**
38) *R. cöhnii*	✓	—	—	✓	—	—	✓	✓	✓	—	75	—	—	75
39) *R. delemar*	—	—	93	93	—	✓	—	✓	✓	93	—	10	—	10
40) *R. delemar* var. *minimus*	—	—	—	—	—	39	—	—	39	93	—	10	—	10
41) *R. delemar* var. *multiplicisporus*	—	—	—	—	—	♦	—	—	39	—	—	10	—	10
42) *R. echinatus*	✓	—	—	✓	—	—	✓	—	✓	—	—	—	—	**?**
43) *R. elegans*	✓	—	—	✓	—	—	—	—	—	—	—	—	—	×
44) *R. equinus*	✓	—	—	—	—	—	69	38	38	—	—	—	—	69
45) *R. equinus* var. *annamensis*	—	—	—	—	—	—	—	—	—	—	—	—	—	**?**
46) *R. formosaensis*	—	—	93	—	—	✓	93	—	93	93	—	—	—	10
47) *R. formosaensis* var. *chlamydosporus*	—	—	93	—	—	39	—	—	93	—	—	—	—	10

Table 1. – continued.

Rhizopus	Lendner 1908	Hanzawa 1915	Yamamoto 1930	Naumov 1939	Kocková-Kratochvílová & Palkoska 1958	Inui *et al.* 1965	Zycha *et al.* 1969	Pidoplichko & Milko 1971	Milko 1974	Schipper 1984	Schipper & Stalpers 1984	Ellis 1985	Ellis 1986	Zheng *et al.* this study
48) *R. fructicola*	—	—	—	—	—	—	—	—	—	—	—	—	—	**?**
49) *R. fusiformis*	—	—	—	✓	—	—	—	93	93	93	—	—	—	9
50) *R. hallerianus*	—	—	—	—	—	—	—	—	—	—	—	—	—	**?**
51) *R. hangchow*	—	—	✓	—	—	—	—	—	93	93	—	—	—	9
52) *R. helminthophthorus*	—	—	—	—	—	—	—	—	—	—	—	—	—	**?**
53) *R. homothallicus*	—	—	—	—	—	—	✓	—	✓	—	✓	—	—	✓
54) *R. homothallicus* var. *indicus*	—	—	—	—	—	—	—	—	53	—	—	—	—	**?**
55) *R. humilis*	—	—	65	—	—	—	—	—	93	—	—	—	—	**?**
56) *R. intermedius*	—	—	—	—	—	—	—	—	—	—	—	—	—	**?**
57) *R. japonicus*	✓	✓	93	✓	—	✓	—	✓	✓	93	—	—	—	10
58) *R. japonicus* var. *angulisporus*	—	—	—	—	—	—	—	—	39	—	—	—	—	**?**
59) *R. javanicus*	—	—	—	—	—	✓	—	57	57	93	—	—	—	10
60) *R. javanicus* var. *kawasakiensis*	—	—	—	—	—	39	—	—	57	93	—	10	—	10
61) *R. javensis*	—	—	—	—	—	—	—	—	✓	—	—	—	—	×
62) *R. kansho*	—	—	87	—	—	57	—	—	93	—	—	—	—	12
63) *R. kasanensis*	—	✓	—	✓	—	—	—	93	93	93	—	—	—	9
64) *R. lendneri*	—	—	—	—	—	—	—	—	—	—	—	—	—	**?**
65) *R. liquifaciens*	—	—	✓	—	—	—	—	—	93	93	—	—	—	0
66) *R. lutescens*	—	—	—	—	—	—	—	—	—	—	—	—	—	×
67) *R. maydis*	—	—	9	✓	—	—	9	93	93	93	—	—	—	9
68) *R. megasporus*	—	—	—	—	—	—	—	93	93	—	—	—	—	9
69) *R. microsporus*	✓	—	—	✓	—	93	✓	✓	✓	—	✓	✓	✓	✓
70) *R. microsporus* var. *azygosporus* [(G. F. Yuan & S. C. Jong) R. Y. Zheng]	—	—	—	—	—	—	—	—	—	—	—	—	—	◊
71) *R. microsporus* var. *azygosporus* [Schwertz *et al.*]	—	—	—	—	—	—	—	—	—	—	—	—	—	70
72) *R. microsporus* var. *chinensis*	—	—	—	—	—	—	—	—	—	—	◊	—	✓	✓
73) *R. microsporus* var. *oligosporus*	—	—	—	—	—	—	—	—	—	—	◊	—	✓	✓
74) *R. microsporus* var. *pseudochinensis*	—	—	—	—	—	—	—	—	—	—	—	—	—	75
75) *R. microsporus* var. *rhizopodiformis*	—	—	—	—	—	—	—	—	—	—	◊	—	✓	✓
76) *R. microsporus* var. *tuberosus*	—	—	—	—	—	—	—	—	—	—	—	—	—	✓
77) *R. minimus*	✓	—	—	✓	—	—	69	69	69	—	—	—	—	**?**
78) *R. mochii*	—	—	87	—	—	—	—	—	93	—	—	—	—	9
79) *R. necans*	—	—	—	✓	—	—	—	—	—	—	—	—	—	122
80) *R. niger*	✓	—	✓	—	—	—	81	—	—	—	—	—	—	**?**
81) *R. nigricans*	✓	—	✓	✓	✓	✓	✓	✓	✓	122	—	—	—	122
82) *R. nigricans* var. *luxurians*	—	—	—	—	—	—	—	—	81	—	—	—	—	122
83) *R. nigricans* var. *minor*	—	—	—	—	—	—	—	—	81	—	—	—	—	**?**
84) *R. nigricans* var. *minutus*	—	—	—	—	—	—	—	—	—	—	—	—	—	**?**
85) *R. nigricans* var. *verticillatum*	—	—	—	—	—	—	—	—	93	—	—	—	—	**?**
87) *R. niveus*	—	—	✓	—	—	✓	—	89	89	—	—	—	—	✓
87) *R. nodosus*	✓	✓	✓	✓	—	93	9	93	93	93	—	—	—	9
88) *R. norvegicus*	—	—	—	—	—	—	—	—	93	—	—	—	—	×
89) *R. oligosporus*	✓	—	—	✓	✓	—	✓	✓	✓	—	73	—	—	73
90) *R. oligosporus* var. *glaber*	—	—	—	—	—	—	—	—	89	—	—	—	—	73
91) *R. olivacellus*	—	—	—	✓	—	—	—	—	—	—	—	—	—	**?**
92) *R. oryzae* [G. Winter]	—	—	—	—	—	—	—	—	—	—	—	—	—	×
93) *R. oryzae* [Went & Prins. Geerl.]	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	—	9	—	9

Table 1. – continued.

Rhizopus	Lendner 1908	Hanzawa 1915	Yamamoto 1930	Naumov 1939	Kocková-Kratochvílová & Palkoska 1958	Inui *et al.* 1965	Zycha *et al.* 1969	Pidoplichko & Milko 1971	Milko 1974	Schipper 1984	Schipper & Stalpers 1984	Ellis 1985	Ellis 1986	Zheng *et al.* this study
94) *R. oryzae* var. *araneosus*	—	—	—	—	—	39	—	—	93	—	—	—	—	10
95) *R. parasiticus*	◊	—	—	—	—	—	—	—	—	—	—	—	—	×
96) *R. peka* I [*R. peka*]	—	—	✓	—	—	—	—	—	39	93	—	—	—	73
97) *R. peka* II	—	—	93	—	—	93	—	—	93	93	—	—	—	9
98) *R. pestis-bovinae*	—	—	—	—	—	—	—	—	—	—	—	—	—	**?**
99) *R. pseudochinensis*	—	—	✓	—	—	✓	—	38	38	93	—	—	—	75
100) *R. pseudochinensis* var. *thermosus*	—	—	—	—	—	—	—	—	93	—	72	—	—	73
101) *R. pusillus*	—	—	—	✓	—	—	9	38	38	—	75	—	—	75
102) *R. pygmaeus*	—	—	—	✓	—	—	—	38	38	—	72	—	—	73
103) *R. ramosus* [(Lindt) *Zopf*]	—	—	—	—	—	—	9	—	—	—	—	—	—	×
104) *R. ramosus* [Moreau]	—	—	—	✓	—	—	9	—	—	—	—	—	—	×
105) *R. reflexoides*	—	—	—	✓	—	—	37	81	81	—	—	—	—	106
106) *R. reflexus*	✓	—	✓	✓	—	✓	37	81	84	124	—	—	—	✓
107) *R. rhizopodiformis*	—	—	—	—	—	—	—	—	—	—	75	—	—	75
108) *R. sakuranei*	—	—	—	—	—	—	—	—	—	—	—	—	—	**?**
109) *R. sakuranei* var. *instriatus*	—	—	—	—	—	—	—	—	—	—	—	—	—	**?**
110) *R. salebrosus*	—	—	—	—	—	—	—	—	93	—	—	—	—	10
111) *R. salebrosus* var. *instriatus*	—	—	—	—	—	—	—	—	93	—	—	—	—	**?**
112) *R. schipperae*	—	—	—	—	—	—	—	—	—	—	—	—	—	✓
113) *R. schizans*	—	—	—	✓	—	—	—	—	—	—	—	—	—	9
114) *R. semarangensis*	—	—	—	—	—	✓	—	—	69	93	—	—	—	9
115) *R. septatas*	—	—	—	—	—	—	—	—	—	—	—	—	—	10
116) *R. sexualis*	—	—	—	—	—	✓	✓	14	14	✓	—	—	—	✓
117) *R. sexualis* var. *americanus*	—	—	—	—	—	—	—	—	14	✓	—	—	—	6
118) *R. shanghaiensis*	—	—	✓	—	—	—	—	—	57	93	—	—	—	9
119) *R. sinensis*	—	—	—	—	—	—	—	—	38	—	—	—	—	72
120) *R. sontii*	—	—	—	—	—	—	—	57	57	93	—	—	—	10
121) *R. speciosus*	◊	—	—	✓	—	—	69	—	—	—	—	—	—	**?**
122) *R. stolonifer*	—	—	—	—	—	—	—	81	81	✓	—	—	✓	✓
123) *R. stolonifer* var. *luxurians*	—	—	—	—	—	—	—	—	—	—	—	—	—	×
124) *R. stolonifer* var. *lyococcos*	—	—	—	—	—	—	—	—	—	✓	—	—	—	106
125) *R. stolonifer* var. *reflexus*	—	—	—	—	—	—	—	—	—	—	—	—	—	106
126) *R. subtilis*	—	—	—	—	—	—	—	—	—	—	—	—	—	**?**
127) *R. suinus*	—	—	—	—	—	—	38	38	38	93	—	—	—	**?**
128) *R. suinus* f. *sterilis*	—	—	—	—	—	—	—	—	—	—	—	—	—	**?**
129) *R. tamari*	✓	—	—	✓	—	57	—	57	57	—	—	—	—	12
130) *R. tanekoji*	—	—	—	—	—	—	—	—	93	—	—	—	—	**?**
131) *R. thermosus*	—	—	87	—	—	57	—	57	57	93	—	—	—	10
132) *R. tonkinensis*	✓	✓	93	✓	—	93	—	—	93	93	—	—	—	12
133) *R. tritici*	✓	✓	✓	✓	—	93	—	93	93	93	—	—	—	9
134) *R. trubini*	—	✓	—	✓	—	—	—	93	93	—	—	—	—	9
135) *R. umbellatus*	—	—	—	—	—	—	—	—	—	—	—	—	—	**?**
136) *R. usamii*	—	✓	—	✓	—	93	—	93	93	93	—	—	—	9

♦ First published as a new taxon; ◊ first published as a new combination; ✓ accepted; **?** doubtful; × excluded; — not mentioned; numeral, treated as synonym of the name in the left column.

ences, Beijing, China. Dried cultures are deposited in the Herbarium Mycologicum Instituti Microbiologici Academiae Sinicae (HMAS), also of the same institute mentioned above.

Isolation

Strains found in China were isolated directly from faded flowers, animal excrements, animal and plant debris, fruits, foods, koji, and other substrates and kept in moist chambers or placed on agar plates. For particulate material like soil, grains, seeds and chaff, the soil plate method of Warcup (1950) was used.

Media and cultivation

PDA (pH7) was used for morphological studies of the sporangial and zygosporic states, mating experiments, isolation and maximum growth temperature tests. In mating experiments, to ensure better formation of zygospores, 0.1 % lecithin was added to the PDA before sterilization and the edge of the petri dishes was sealed with parafilm to maintain moisture after the two mating partners were inoculated. Cultivation period and temperature were 4–7 days at 22–24 °C, 26–28 °C, and 30–32 °C for *R. stolonifer* & allies, *R. arrhizus* & allies, and *R. microsporus* & allies for morphological studies of the sporangial state; 10–15 days at 19–21 °C, 23–25 °C, and 27–29 °C respectively for the three groups of *Rhizopus* for morphological studies of the zygosporic state and mating experiments, 3–5 days at 24–28 °C for isolation, and 4–7 days at different temperatures between 25 °C and 55 °C for maximum growth temperature tests.

Observation and description

When studying the sporangial state morphology, at least two cultures were grown for each strain and at least 2–4 sites from each culture were chosen for daily microscopical examination throughout the 4th to 7th day after inoculation. Descriptions of the sporangial state of all taxa were based on a comprehensive study of all strains. Since mating compatibility seemed to be quite weak in all strains studied, description of the zygosporic state of a certain taxon was based on a composite study of all zygospore-forming strains of the same taxon.

Results and Discussion

Maximum growth temperature

A total of 203 strains representing the 17 taxa of *Rhizopus* were tested twice for their maximum growth temperature. For *R. arrhizus*

A. Fisch. var. *arrhizus, R. arrhizus* var. *delemar* (Boidin) J. J. Ellis, *R. arrhizus* var. *tonkinensis* (Vuill.) R.Y. Zheng & X. Y. Liu, and *R. stolonifer* (Ehrenb.) Vuill., 35, 30, 30 and 32 strains, respectively, were tested. For the other taxa with less than 30 strains available, all strains of each taxon were tested. Results obtained are shown in Table 2.

In our study on the genus *Cunninghamella*, we have found that each taxon can be characterized by its specific range of maximum growth temperature (Zheng & Chen 2001). In the present study, only one strain was found in many taxa of *Rhizopus* like *R. americanus* (Hesselt. & J. J. Ellis) R. Y. Zheng, G. Q. Chen & X. Y. Liu, *R. caespitosus* Schipper & Samson, *R. homothallicus* Hesselt. & J. J. Ellis, *R. microsporus* var. *azygosporus* (G. F. Yuan & S. C. Jong) R. Y. Zheng, *R. microsporus* var. *tuberosus* R. Y. Zheng & G. Q. Chen, *R. schipperae* Weitzman *et al.*, and *R. sexualis* (G. Sm.) Callen, for which no specific ranges of their maximum growth temperature could be sorted out. But if the maximum growth temperature is analyzed for groups of more closely related taxa like *R. stolonifer* and its allies, *R. arrhizus* and its allies, *R. microsporus* and its allies, group-specific ranges can be summarized. The maximum growth temperature ranges for *R. stolonifer* and its allies, *R. arrhizus* and its allies, and *R. microsporus* and its allies are, respectively, (26–) 27–32 (–33) °C, (37–) 39–41 (–42) °C, and (40–) 45–49 (–51) °C. However, there are three exceptions: the maximum growth temperatures of *R. homothallicus, R. microsporus* var. *tuberosus* and *R. niveus* M. Yamaz, which should be assigned to *R. microsporus* and its allies on a morphological base, are 40–42 (–43) °C and come close to the range of *R. arrhizus*. In molecular systematic studies, *R. homothallicus* and *R. microsporus* var. *tuberosus* closely relate to *R. microsporus* and its allies, but *R. niveus* relates more closely to *R. arrhizus* (Liu *et al*. 2007a).

Mating experiments

As mentioned in the above paragraph, among the 17 taxa accepted here, seven taxa are represented by one strain only, hence, they do not have a mating partner. Fortunately, three of them, *R. americanus, R. homothallicus,* and *R. sexualis,* are homothallic and enable us to study their zygosporic states. In the remaining ten taxa, after thousands of experiments on intraspecific and intravarietal matings have been made, zygospores were formed by strains of five taxa: *R. microsporus* Tiegh. var. *microsporus, R. microsporus* var. *chinensis* (Saito) Schipper & Stalpers, *R. microsporus* var. *rhizopodiformis* (Cohn) Schipper & Stalpers, *R. reflexus* Bainier, and *R. stolonifer.* No zygospores were formed by *R. arrhizus* var. *arrhizus, R. arrhizus* var. *delemar, R. arrhizus* var. *tonkinensis, R. microsporus*

Table 2. Maximum growth temperature (°C) of the strains of accepted *Rhizopus* taxa.

***R. americanus* [27]**							
NRRL 2626(T)	27, 27						
***R. arrhizus* var. *arrhizus* [39–42]**							
CBS 110.17	41, 41	CBS 112.07	40, 41	CBS 258.28	41, 42	CBS 260.28	42, 42
CBS 264.28	41, 42	CBS 266.30	41, 41	CBS 387.34	41, 42	CBS 395.34	40, 39
HUT 1256	41, 41	HUT 1285	40, 41	HUT 1294	41, 41	IFO 4798	41, 41
IFO 4809	40, 41	IFO 5414	40, 41	JCM 5577	41, 41	JCM 5580	41, 41
JCM 5581	42, 41	JCM 5584	41, 41	JCM 5590	40, 41	NRRL 1469(NT)	39, 40
NRRL 3133	40, 41	NRRL 5866	39, 39	R-55	39, 40	R-141	41, 41
R-143	40, 42	R-152	40, 41	R-166	41, 41	R-171	40, 40
R-177	40, 40	R-199	39, 40	R-209	40, 40	R-226	41, 40
R-237	40, 40	R-612	39, 40	R-613	39, 40		
***R. arrhizus* var. *delemar* [(38–)39–41(–42)]**							
CBS 279.38	41, 41	CBS 295.31	41, 41	CBS 385.34	40, 40	CBS 386.34	39, 40
CBS 389.34	39, 40	CBS 391.34	39, 41	CBS 393.34	41, 41	CBS 402.51	40, 38
CBS 406.51	40, 38	HUT 1220	39, 40	HUT 1255	40, 41	IFO 4697	41, 41
IFO 4726	40, 40	IFO 4735	40, 40	IFO 4770	41, 41	IFO 4801	41, 40
IFO 5442	41, 41	JCM 5560	41, 39	JCM 5561	42, 41	JCM 5564	40, 38
NRRL 1472(T)	39, 40	NRRL 2872	40, 40	R-27	41, 41	R-28	39, 40
R-29	41, 40	R-30	39, 40	R-33	40, 41	R-34	42, 41
R149	40, 41	R-248	40, 40				
***R. arrhizus* var. *tonkinensis* [(39–)40–42]**							
CBS 257.28	40, 41	CBS 330.53	40, 41	HUT 1235	41, 41	IFO 4716	40, 41
IFO 5318	41, 41	IFO 5384	41, 41	IFO 5438(T)	40, 41	IFO 5780	40, 40
JCM 5569	41, 41	JCM 5570	41, 40	NRRL 2710	41, 41	R-42	41, 40
R-155	41, 41	R-161	42, 42	R-165	41, 42	R-170	40, 40
R-178	41, 41	R-180	42, 41	R-183	40, 40	R-187	40, 40
R-189	40, 39	R-198	41, 41	R-205	41, 41	R-208	41, 41

Table 2. – continued.

R-212	41, 41	R-220	42, 42	R-487	42, 42	R-495	42, 42
R-519	41, 41	R-534	41, 41				
***R. caespitosus* [48]**							
CBS 427.87(T)	48, 48						
***R. homothallicus* [43]**							
CBS 336.62(T)	43, 43						
***R. microsporus* var. *microsporus* [46–48]**							
CBS 699.68(NT)	48, 47	CBS 700.68	48, 48	R-39	48, 48	R-41	48, 47
R-43	47, 47	R-44	46, 46	R-45	46, 46	R-46	46, 47
R-139	48, 48	R-218	46, 46	R-221	48, 48	R-222	48, 48
R-223	49, 49	R-225	48, 48	R-227	48, 48	R-228	47, 47
R-229	47, 46	R-230	47, 47	R-232	47, 47	R-233	46, 46
R-236	47, 46	R-242	47, 47	R-243	47, 46	R-244	47, 47
R-245	48, 47						
***R. microsporus* var. *azygosporus* [49]**							
CBS 357.93(T)	49, 49						
***R. microsporus* var. *chinensis* [46–48]**							
CBS 294.31	49, 48	CBS 631.82(T)	48, 47	IFO 30499	48, 47	R-36	46, 46
R-48	48, 48	R-214	48, 48	R-217	48, 48	R-224	48, 48
R-234	48, 48	R-235	48, 48				
***R. microspoorus* var. *oligosporus* [(45–)46–49]**							
CBS 337.62	47, 47	CBS 338.62	46, 45	CBS 339.62(NT)	47, 46	CBS 344.29	49, 49
CBS 394.34	49, 48	IFO 8631	46, 47	IFO 31987	46, 47	IFO 32002	46, 47
IFO 32003	47, 47	JCM 5596	47, 47	R-47	46, 46	R-65	46, 46
R-216	46, 46						

Table 2. – continued.

***R. microsporus* var. *rhizopodiformis* [(45–)46–51]**							
CBS 343.29	51, 50	CBS 388.34	47, 48	CBS 536.80(NT)	51, 50	HUT 1231	46, 45
JCM 5585	50, 49	R-49	49, 49	R-52	50, 49	R-181	47, 48
R-219	50, 49	R-231	47, 46	R-238	51, 50	R-246	46, 47
***R. microsporus* var. *tuberosus* [47]**							
R-215(T)	47, 47						
***R. niveus* [42]**							
IFO 4759(T)	42, 42	IFO 4810	42, 42				
***R. reflexus* [(31–)32–33]**							
CBS 319.35	33, 32	CBS 320.35	33, 33	HUT 1273	33, 33	JCM 5589(T)	32, 31
R-11	33, 32	R-12	33, 32	R-709	33, 32		
***R. schipperae* [45]**							
ATCC 96514(T)	45, 45						
***R. sexualis* [26–27]**							
NRRL 2567(T)	27, 26						
***R. stolonifer* [(30–)31–32]**							
CBS 107.76	31, 31	CBS 108.76	31, 31	IFO 4781(NT)	31, 32	IFO 5781	31, 31
IFO 30795	31, 30	R-146	31, 31	R-151	32, 32	R-154	31, 31
R-164	31, 31	R-169	32, 32	R-173	32, 31	R-175	31, 31
R-182	32, 32	R-185	32, 32	R-188	31, 31	R-190	32, 32
R-194	32, 31	R-201	31, 31	R-204	30, 30	R-250	32, 32
R-252	32, 31	R-259	32, 32	R-262	31, 31	R-551	31, 31
R-563	31, 32	R-568	32, 32	R-572	32, 32	R-575	32, 31
R-577	31, 31	R-579	32, 31	R-581	32, 31	R-582	31, 31

var. *oligosporus* (Saito) Schipper & Stalpers, and *R. niveus*. Numerous experiments on interspecific and intervarietal matings among all the 17 taxa have also been conducted. Strains of nine taxa did not react with any other strain: *R. americanus, R. arrhizus* var. *arrhizus, R. arrhizus* var. *delemar, R. arrhizus* var. *tonkinensis, R. caespitosus, R. homothallicus, R. niveus, R. schipperae,* and *R. sexualis*. Strains of the remaining eight taxa reacted with 1–9 strains of other taxa and formed azygospores, gametangia, or zygosporangia as follows: *R. microsporus* var. *microsporus* – CBS 699.68 (+) × CBS 388.34 (–) (*R. microsporus* var. *rhizopodiformis*), CBS 700.68 (–) × JCM 5589 (+) (also *R. microsporus* var. *rhizopodiformis*), resulted in azygospore formation, and CBS 700.68 (–) × R-215 (+) (*R. microsporus* var. *tuberosus*), resulted in zygosporangium formation. *R. microsporus* var. *azygosporus* – CBS 357.93 (+) × CBS 388.34 (–) (*R. microsporus* var. *rhizopodiformis*) resulted in zygosporangium formation. *R. microsporus* var. *chinensis* – CBS 294.31 (+) × CBS 388.34 (–) (*R. microsporus* var. *rhizopodiformis*) resulted in zygosporangium formation. *R. microsporus* var. *oligosporus* – CBS 344.29 (+) × CBS 388.34 (–) (*R. microsporus* var. *rhizopodiformis*) resulted in zygosporangium formation. *R. microsporus* var. *rhizopodiformis* – JCM 5585 (+) × CBS 700.68 (–) (*R. microsporus* var. *microsporus*) and CBS 388.34 (–) × CBS 699.68 (+) (also *R. microsporus* var. *microsporus*) resulted in azygospore formation; CBS 388.34 (–) × CBS 357.93 (+) (*R. microsporus* var. *azygosporus*), CBS 388.34 (–) × CBS 294.31 (+) (*R. microsporus* var. *chinensis*); and CBS 388.34 (–) × CBS 344.29 (+) (*R. microsporus* var. *oligosporus*) resulted in zygosporangium formation. *R. microsporus* var. *tuberosus* – R-215 (+) × CBS 700.68 (–) (*R. microsporus* var. *microsporus*) resulted in zygosporangium formation. The last two taxa, *R. reflexus* and *R. stolonifer* reacted to each other only and not to any other taxa – CBS 319.35 (+) × CBS 107.76 (–), R-11 × CBS 107.76 (–), CBS 320.35 (–) × R-185 (+), and HUT 1235 (–) × CBS 108.76 (+) resulted in gametangium formation; while CBS 319.35 (+) × IFO 4781 (–), JCM 5589 (+) × CBS 107.76 (–), JCM 5589 (+) × IFO 4781, JCM 5589 (+) × R-173 (–), CBS 320.35 (–) × CBS 108.76 (+) resulted in zygosporangium formation.

The mating ability of most *Rhizopus* strains seems to be very weak when compared with that of *Cunninghamella*. In *Cunninghamella* (Zheng & Chen 2001), the mating type (+ or –) is easy to determine, because most strains will generally response to the tester of opposite mating type by forming zygosporangia or at least gametangia in intraspecific and intravarietal matings, even in interspecific and intervarietal matings. A possible explanation for the low mating ability of *Rhizopus* strains might be that many strains of different taxa of the genus have lost to some degree or entirely their mating ability while adopting to artificial environments (e.g. in fer-

mentation processes). This may explain why strains of the three *R. arrhizus* varieties did not form zygospores themselves and did not response to each other or any other strain in all crosses.

Morphological studies

Like in other genera of the Mucorales, taxonomy of *Rhizopus* is principally based on anamorphic morphology. The followings are the characteristics adopted by most scientists: branching pattern and abundance of rhizoids; number per group, length, width, and straightness of the sporangiophores; diameter and colour of the sporangia; size and shape of the columellae; size, striation, and surface ornamentation (SEM observations) of the sporangiospores, etc. As for the teleomorphs, only the type of sexual reproduction; size and colour of the zygosporangia; and equality of the two suspensors supporting a zygosporangium are taken into consideration.

In addition to the above characteristics, we have found many more criteria, which are summarized in the synoptic key, in both the anamorphic and teleomorphic states, useful for classifying species and varieties in *Rhizopus*. Some of these criteria, like the equality of width throughout the sporangiophores, origin of sporangiophores, etc., are of universal significance to many taxa. Others, though not universal, are still very effective in distinguishing one to several taxa. For example, the hyphal knots on aerial mycelia of *R. niveus* are not found in any other taxa; the giant cells on aerial mycelia can only be found in *R. americanus* and *R. sexualis*. Morphology of the teleomorphs is much less complex than that of the anamorphs, but there are still many characters suitable as taxonomic criteria. The zygospores of most taxa are colourless, however, we have noticed that the zygospores of *R. americanus* and *R. sexualis* are respectively greenish and brownish and very different from all the other taxa.

Like our previous study on *Cunninghamella* (Zheng & Chen 2001), we have found that, the more criteria being applied to study the taxonomy of *Rhizopus*, the more satisfactory results could be obtained. It is very difficult to use only one criterion to distinguish taxa in this genus.

Generally speaking, morphological studies are well supported by our studies on other aspects with very few exceptions. *R. homothallicus* and *R. niveus* are morphologically more closely related to species like *R. caespitosus, R. microsporus,* and *R. schipperae,* but their maximum growth temperatures are within the range of *R. arrhizus*. Our results of sequence analyses have also shown that *R. niveus* is in close affinity to *R. arrhizus* although it is not so in morphology.

Taxonomy

Rhizopus Ehrenb., Nova Acta Acad. Caes. Leop.-Carol. 10: 198. 1821. (nom. cons.)

= *Ascophora* Tode, Fungi Mecklenb. Sel. 1: 13. 1790 : Fr., Syst. Mycol. 3: 309. 1832. (nom. rej.)

= *Mucor* Mich. ex L., Sp. Pl. 2: 1185. 1753 : Fr., Syst. Mycol. 3: 317. 1832. (p. p.)

= *Pilophora* Wallr., Flora Kryptog. Germ. II, 4: 332. 1833. (nom. illeg., Art. 53.1), non Jacq., 1802 (Palmae). Hesselt., Mycologia 47: 349. 1955. (as "*Philophora*").

= *Chlamydomucor* Bref., Unters. Gesam. Mykol. 8: 223. 1889. (p. p.)

= *Amylomyces* Calmette, Ann. Inst. Pasteur 6: 611. 1892.

= *Crinofera* Nieuwl., Amer. Midl. Nat. 4: 383. 1916.

Colonies usually deep gray to blackish, rarely remaining white in colour after maturity, growing rapidly at appropriate temperatures. Stolons on aerial mycelia are well or poorly developed, septate or not. Rhizoids developed from stolons and opposite sporangiophores, rhizopodiformis or finger-like, abundant to scarce, sometimes absent. Sporangiophores typically arising from stolons, sometimes from hyphae, rarely from rhizoids, solitary or 2–10 or more in groups, often straight to subcurved, nodding in some strains, mostly simple, sometimes forked at the upper part or rarely at the basal part, equal in width throughout, tapering or widening upwards, or unequal at places, smooth to minutely verruculose. Apophyses always present, evident to less evident. Sporangia globose to subglobose, brown to dark brown, deliquescing or breaking in water, leaving or not leaving a small collar. Columellae well developed, variously shaped, subhyaline to grayish brown, smooth to verruculose. Sporangiospores numerous in a sporangium, regular or irregular in shape and size, smooth to angulate, with distinct to faint, or invisible striation. Chlamydospores on mycelia present or absent, mostly intercalary, solitary, in short chains, or in mass. Giant cells on mycelia present or absent. Zygosporangia globose to somewhat depressed globose, brown, reddish brown, or blackish brown, covered with blunt to pointed projections. Azygosporangia when formed, similar in outlook to zygosporangia. Zygospores formed or not formed in both zygosporangia and azygosporangia, always solitary, globose to broadly ovoid, outer wall thin to thick, crenulate to tuberose, mostly hyaline, rarely palely coloured, with or without a large central oil globule. Suspensors in pairs when supporting a true zygosporangium, single when supporting an azygosporangium, the two suspensors supporting a zygosporangium equal in shape and size, or equal in shape but unequal in size, or unequal in shape and size, inflated or not inflated, constricted or not constricted at the base, incrusted or not

incrusted, septate or not septate, hyaline, brownish, or orange brown. Homothallic or heterothallic.

Maximum growth temperature: 26–51 °C

DNA length of respectively entire ITS region (including 5.8S), *pyrG* gene intron 1 and intron 2: 450–788, 46–82, 0–71 bp.

G + C mol%: 37–42

Type species: *Rhizopus nigricans* Ehrenb., nom. illegit.

***R. stolonifer* (Ehrenb.: Fr.) Vuill.** (≡ Mucor stolonifer Ehrenb.: Fr.)

Rhizopus Ehrenb. and *Mucor* Fresen. were conserved simultaneously over *Ascophora* Tode and *Mucor* Micheli ex L. in two important proposals made by Kirk (1986). For the details, please see Taxon 35: 371–377, 1986.

Rhizopus has been placed under Mucoraceae by most authors in either early or recent works (Lendner 1908, Naumov 1939, Hesseltine 1955, Inui *et al.* 1965; Zycha *et al.* 1969, Milko 1974, Kirk *et al.* 2001, Kirk & Benny 2004). In 1982, Arx seggregated the following genera – *Absidia, Actinomucor, Amylomyces, Chlamydoabsidia, Circinella, Dicranophora, Gongronella, Halteromyces, Pirella, Rhizopodopsis, Rhizopus, Thermomucor, Sporodiniella,* and *Syzygites* from Mucoraceae to establish the new family Absidiaceae. Benny & Benjamin (1993) seem to be the only authors who accepted this new family. Although the authors of these two papers included different genera in Absidiaceae, both of them assigned *Rhizopus* to the new family.

The species number of *Rhizopus* is quite small; still many authors prefer to divide them into sections or groups before dividing into species.

Naumov (1939) described three formal sections to accommodate the species he accepted – Sect. I. Ehrenbergia N. Naumov: "Sterile aerial mycelia absent, distinctly differentiate into stolons, sporangiophores and rhizoids; lateral sporangiophores almost completely absent, sporangiophores erect; sporangia large; capacity of propagation intense and repeatedly growing." Species included: *R. nigricans* Ehrenb., *R. artocarpi* Racib., *R. echinatus* Tiegh., and *R. angulisporus* (Saito) Naumov (pertaining to the *R. stolonifer* Group). Sect. II. Hanzawia N. Naumov: "Sterile aerial mycelia present, less distinctly differentiate into stolons, sporangiophores and rhizoids; lateral sporangiophores frequent; sporangia and spores medium sized; capacity of propagation weak, not repeatedly growing." Species included: *R. oryzae* Went & Prins. Geerl., *R. arrhizus, R. japonicus* Vuill., *R. batatas* Nakaz., *R. chinensis* Saito, *R. cambodja* (Chrzaszcz) Vuill., *R. cohnii* Berl. & De Toni, *R. kazamensis* Hanzawa, *R. nodosus* Namysl., *R. oligosporus* Saito, *R. ramosus* (Lindt) Zopf, *R. reflexus, R. reflexoides* Philippow, *R. tamari* Saito, *R. tonkinensis* Vuill., *R. tritici* Saito, *R. trubini* Hanzawa, *R. usamii* Hanzawa, and *R. maydis* Bruderl. (per-

taining to the *R. arrhizus* Group, *R. microsporus* Group, and also *R. stolonifer* Group). Sect. III. Van Tieghemia N. Naumov: "Species distinguished by the smaller proportions of all parts; colonies low, sporangiophores short, spores small". Species included: *R. microsporus, R. minimus* Tiegh., *R. circinans* Tiegh., *R. pusillus* Naumov, and *R. pygmaeus* Naumov (pertaining to the *R. microsporus* Group).

According to Schwertz *et al.* (1997), Scholer (1970) was the first who erected the *R. microsporus* Group characterized by shorter sporangiophores, smaller sporangia, shorter rhizoids with little or no pigments, and with maximum growth temperature of 45 °C or more. On the basis of Scholer's work, Schipper published two papers (Schipper 1984, Schipper & Stalpers 1984) on *Rhizopus*, dividing the taxa into two groups and one species as follows: The *R. stolonifer* Group: "rhizoids complex, well developed; sporangiophores 1–3 (–4) mm long; sporangia (150–) 250–275 (–300) μm diam.; zygospores black, upto 225 μm diam.; suspensors equal; maximum growth temperature (33–) 36 °C; occurring on overripe fruit". Species and varieties included: *R. sexualis* var. *sexualis, R. sexualis* var. *americanus* Hesselt. & J. J. Ellis, *R. stolonifer* var. *stolonifer*, and *R. stolonifer* var. *lyococcos* (Ehrenb.) Stalpers & Schipper. The single species *R. oryzae:* "rhizoids medium; sporangiophores maximum 1–2.5 mm long; sporangia maximum 160–240 μm diam.; zygospores brown, up to 140 μm diam.; suspensors unequal; maximum growth temperature 45 °C; occurring as food fermentors and agents of mucormycosis". Species included: *R. oryzae* only. The *R. microsporus* Group: "rhizoids simple; sporangiophores mostly up to 0.5 mm, rarely up to 1 mm long; sporangia up to 100 μm diam.; zygospores reddish brown, up to 90 (–100) μm diam.; suspensors unequal; maximum growth temperature over 45 °C; occurring as agents of mucormycosis". Species and varieties included: *R. homothallicus, R. microsporus* var. *microsporus, R. microsporus* var. *chinensis, R. microsporus* var. *oligosporus,* and *R. microsporus* var. *rhizopodiformis*.

Frye & Reinhardt (1993) reported that species within the three groups of *Rhizopus* as defined by Schipper (1984) were further grouped by DNA differences. The DNA mol % G + C values of the *R. stolonifer* Group, *R. arrhizus* Group, and *R. microsporus* Group are respectively 37.0–39.3 %, 34.9–36.8 %, and 37.8–40.2 %. Abe *et al.* (2006) also reported that analyses on the rDNA 18S, ITS, 28S D1/D2 sequences of all the *Rhizopus* species accepted by Schipper (1984) and Schipper & Stalpers (1984) resulted in three major clusters corresponding to the *R. stolonifer* Group, *R. oryzae,* and *R. microsporus* Group, although at the same time, they have already noticed that both *R. schipperae* and *R. reflexus* (as *R. stolonifer* var. *lyococcos*) were located in two distinct positions in respectively two or all of the three trees and could not be clustered with either group.

As mentioned above, the number of species in *Rhizopus* is quite small; we think it is unnecessary to add a rank-like group between the genus and the species. In the synoptic key, all criteria are designed on the basis of individual species or varieties instead of groups; while in the dichotomous key, the three groups are keyed out first before individual species or varieties are keyed out, so that people who prefer to divide by groups before dividing into species can use this key. In this paper, descriptions of all taxa are arranged in alphabetic order.

The main difficulties we have encountered include: firstly, most of the ex-type or authentic cultures of the many names published in this genus could not be found anymore; secondly, the vast literatures, especially the old ones, are very difficult to collect. Furthermore, some of the ex-type cultures with the same name but provided by different culture collections were found to be different fungi. Under such circumstances, after studying the ex-type material, we had first to check the morphological characteristics obtained from the so-called ex-type material with those described in its original description before comparison with our strains in order to determine whether the name of the ex-type culture should be included as one of the synonyms of the species under study.

In the present study, 17 taxa are recognized. Among them, *R. americanus* (Zheng *et al.* 2000), *R. arrhizus* var. *tonkinensis* (this study) and *R. microsporus* var. *azygosporus* (this study) are stat. & comb. nov., *R. microsporus* var. *tuberosus* is a recently described variety found in China (Zheng & Chen 1998). The remaining 13 taxa, *R. arrhizus* var. *arrhizus, R. arrhizus* var. *delemar, R. caespitosus, R. homothallus, R. microsporus* var. *microsporus, R. microsporus* var. *chinensis, R. microsporus* var. *oligosporus, R. microsporus* var. *rhizopodiformis, R. niveus, R. reflexus, R. schipperae, R. sexualis*, and *R. stolonifer* are previously recognized taxa. Seventy-two names are treated as synonyms, 25 species, eight varieties and one form are thought to be doubtful, and nine species and four varieties are excluded from the genus. Neotypes are designated for *R. microsporus* var. *microsporus, R. microsporus* var. *oligosporus, R. microsporus* var. *rhizopodiformis,* and *R. stolonifer.*

KEY TO THE TAXA OF *RHIZOPUS* BASED ON THEIR SPORANGIAL AND ZYGOSPORIC CHARACTERISTICS

Synoptic Key

Abbreviations of taxa:

R. americanus	*am*
R. arrhizus var. *arrhizus*	*aa*

R. arrhizus var. *delemar*	*ad*
R. arrhizus var. *tonkinensis*	*at*
R. caespitosus	*ca*
R. homothallicus	*ho*
R. microsporus var. *microsporus*	*mm*
R. microsporus var. *azygosporus*	*ma*
R. microsporus var. *chinensis*	*mc*
R. microsporus var. *oligosporus*	*mo*
R. microsporus var. *rhizopodiformis*	*mr*
R. microsporus var. *tuberosus*	*mt*
R. niveus	*ni*
R. reflexus	*re*
R. schipperae	*sc*
R. sexualis	*se*
R. stolonifer	*st*

SPORANGIAL STATE

I. Colonies (on PDA):
   A. Colour:
      Deep gray to nearly black — *am, aa* (most strains), *ad, at, ca, ho, mm, ma, mc, mo, mr, mt, re, se, st*
      White or dirty white — *aa* (some strains), *ni*
      White and vinaceus in the central part — *sc*
   B. Height:
      Thin (1 layer on Czapek's agar) — *sc*
      1 mm — *mt*
      1–2 mm — *am*
      1–2 (–8) mm — *rh*
      (1–) 2–4 mm — *mo*
      2–5 (–8) mm — *ca, mm, ma, mc*
      4–7 mm — *se*
      6–10 mm — *aa, ad, at, ho, ni*
      6–12 mm — *re, st*
   C. Mycelia:
      Aerial mycelia typically twisted tightly into hyphal knots — *ni*
      Aerial mycelia not twisted tightly into hyphal knots — *am, aa, ad, at, ca, ho, mm, ma, mc, mo, mr, mt, re, sc, se, st*

II. Stolons:
   A. Development:
      Well developed — *am, ca, mm, ma, mc, mo, mr, ni, re, sc, se, st*
      Poorly developed — *aa, ad, at, ho, mt*

B. Outlook:
Normal — *am, aa, ad, at, ca, ho, mm, ma, mc, mo, mr, ni, re, sc, se, st*
Tuberose at places — *mt*

III. Rhizoids:
A. Development:
Well developed — *am, ma, mr, re, se, st*
Less well developed — *ad, at, ca, mm, mc, mo, ni, sc*
Poorly developed — *aa, ho, mt*
B. Branching:
Typically rhizopodiformis — *am, ma, mr, re, se, st*
Typically finger-like — *ca, ho, mm, mc, mo, ni, sc*
Finger-like, rarely rhizopodiformis — *aa, ad, at*
Typically tuberous — *mt*
C. Origin:
Mainly arising from, and opposite stolons — *am, ca, ho, mm, ma, mc, mo, mr, ni, re, sc, se, st*
Arising from stolons and aerial hyphae — *aa, ad, at*
Arising from the tuberose part of stolons — *mt*

IV. Sporangiophores:
A. Number per group:
1, or 2 — *ho*
1, or 2–3 — *am, ni*
1, or 2–3 (–6) — *aa, ad, mm, ma, mc, mr*
1, or 2–4 (–7) — *at, mo, mt*
1, or 2–5 (–9) — *re, st*
1, or 2–8 (–10) — *ca, sc, se*
B. Length:
Mostly within 200 μm, reaching 400 μm or more — *mt*
Mostly within 300 μm, reaching 500 μm or more – *ca, mo, mr, sc*
Mostly within 400 μm, reaching 700 μm or more — *ma, mc*
Mostly within 500 μm, reaching 800 μm or more — *ho, mm, ni*
Mostly within 1000 μm, reaching 1700 μm or more — *aa, ad, at*
Mostly within 1500 μm, reaching 2000 μm or more — *am, re*
Mostly within 2500 μm, reaching 3000 μm or more — *se, st*
C. Width:
Mostly within 9 μm — *sc*
Mostly within 12.5 μm, reaching 15 μm or more — *ca, mm, ma, mt, ni*
Mostly within 20 μm, reaching 26 μm or more — *am, aa, ad, at, ho, mc, mo, mr*
Mostly within 27 μm, reaching 32 μm or more — *re*
Mostly within 32 μm, reaching 41 μm or more — *se*
Mostly within 35 μm, reaching 49 μm or more — *st*

D. Equality in width throughout:
Typically widening upwards — *ho, mc, mt*
Typically tapering upwards — *mm*
Mostly equal, rarely widening upwards — *am, ad, ca, mo, mr, st*
Mostly equal, rarely tapering upwards — *sc*
Equal to subequal — *aa, at, ma, ni, re, se*

E. Septation:
0 — *aa, ad, at, ho, mm, ma, mt, ni, re, st*
0 (–1) — *am, ca, mc, mo, se*
0 (–2) — *mr, sc*

F. Smoothness:
Smooth — *am, ho, mm, ma, mo, mt, ni, sc, se*
Smooth to minutely roughened — *aa, ad, at, ca, mc, mr, re, st*

G. Branching:
Simple — *am, ca, ho, mm*
Simple, sometimes forked at the upper portion — *aa, ad, at, ma, mc, mo, mr, mt, ni, st*
Simple, sometimes forked at the upper portion, rarely verticillate — *se*
Simple, sometimes forked at the base — *sc, re*

H. Origin:
Typically arising from stolons opposite rhizoids — *am, mm, ma, mr, re, sc, st*
Mostly arising from stolons opposite rhizoids, sometimes from aerial hyphae — *ad, at, mc, mo, ni, se*
Often from aerial hyphae, also from stolons opposite rhizoids — *aa, ho, mt*
Mostly arising from stolons opposite rhizoids, rarely directly from rhizoids – *ca*

I. Swellings:
Absent — *am, ca, ho, mm, ma, mc, mo, mr, re, sc, se, st*
Occasionally present — *at, mt, ni*
Common, mostly at the middle portion — *aa*
Common, mostly at the apex or the middle portion — *ad*

J. Straightness:
Straight or curved, not nodding — *am, ca, ho, mm, ma, mc, mo, mr, mt, ni, sc, st*
Straight or curved, sometimes nodding — *re*
Straight or curved, sometimes undulate or geniculate — *aa, ad*
Straight or curved, sometimes undulate, rarely helicoid — *at*
Straight or curved, sometimes vigorously recurved — *se*

V. Sporangia:

A. Diameter:
Mostly less than 60 μm, reaching 70 μm — *sc*
Mostly less than 70 μm, reaching 80 μm — *ca*

Mostly less than 90 μm, reaching 110 μm — *mo, ni*
Mostly less than 100 μm, reaching 120 μm — *mm, mc, mr, mt*
Mostly less than 110 μm, reaching 130 μm — *ma*
Mostly less than 120 μm, reaching 150 μm — *am, ho*
Mostly less than 190 μm, reaching 235 μm — *aa, ad, at, se*
Mostly less than 220 μm, reaching 280 μm — *re, st*

B. Deliquescence:
Quickly deliquescing — *am, ca, ho, ma, mt, re, sc, se, st*
Slowly deliquescing — *aa, mm, mc, mo, mr*
Quickly to slowly deliquescing — *ad, at*
Deliquescing or breaking — *ni*

VI. Apophyses:
A. Conspicuous — *aa, ad, at, ho, mc, mo, mr, mt, ni, re, se, st*
B. Inconspicuous — *am, ca, mm, ma, sc*

VII. Collars:
A. With or without a collar — *am, at, ca, ho, ma, mc, mo, mr, ni*
B. Usually without a collar — *aa, ad, mm, mt, re, sc, se, st*

VIII. Columellae:
A. Shape:
Typically pyriform, others ellipsoid or ovoid, roundish conical, etc. — *ma, mr*
Typically globose to subglobose, others ellipsoid, ovoid, roundish conical, etc. — *ca, ho, mm, ni*
Typically ovoid or ellipsoid, others roundish conical, rarely subglobose, etc. — *am, ad, mc, mt, re, st*
Typically strictly ovoid and with a narrow base, others globose or roundish conical — *at*
Typically roundish conical or broadly ovoid, rarely subglobose — *aa, sc*
Typically with some not symmetrical and askew — *mo, se*

B. Smoothness:
Smooth — *am, aa, ad, at, ca, mm, ni, re, sc, se, st*
Smooth, rarely roughened at the apex — *ho, ma, mr*
Smooth in the larger ones and roughened in the smaller ones — *mc, mo, mt*

C. Size (when not globose):
Less than 40 × less than 35 μm — *sc*
Less than 60 × less than 55 μm — *ca, mt*
Less than 70 × less than 60 μm — *ho, mo, ni*
Less than 90 × less than 80 μm — *mm, mc*
Less than 105 × less than 90 μm — *ma, mr*
Less than 130 × less than 120 μm — *am*
Less than 180 × less than 140 μm — *se*
Less than 190 × less than 180 μm — *aa, ad*
Less than 210 × less than 190 μm — *at, re, st*

D. Diameter (when globose):
Less than 40 μm — *sc*
Less than 50 μm — *mt*
Less than 60 μm — *ca, mr*
Less than 70 μm — *mc, ni*
Less than 80 μm — *ho, mm, ma, mo*
Less than 130 μm — *am*
Less than 140 μm — *re, se*
Less than 150 μm — *ad*
Less than 170 μm — *aa*
Less than 190 μm — *at, st*

IX. Sporangiospores:
A. Shape:
Ovate, globose or subglobose — *am, aa, at, ca, ho, mm, ma, mc, mr, ni, re, sc, st*
Ovate, globose, subglobose, and irregular — *ad, mo, mt, se*
B. Angulation:
Smooth to subsmooth — *am, ca, ho, mm, ma, mc, mr, sc*
Subsmooth to subangulate — *aa, ad, at, mo, mt, ni, re, se, st*
C. Striation:
Quite evident — *aa, ad, at, mm, re, se, st*
Very faint to nearly invisible — *am, ca, ho, ma, ni, sc*
Almost invisible — *mc, mo, mr, mt*
D. Size (when ovoid or irregular):
Mostly 4–7 (–8) μm in length — *mm, ma, mr, sc*
Mostly 5–8 (–10) μm in length — *aa, at, ca, ho, mc*
Mostly 5–9 (–12.5) μm in length — *ni*
Mostly 5–9 (–14.5) μm, and when irregular reaching 53 μm in length — *ad, mo*
Mostly 5.5–10 μm and when irregular reaching 20 μm in length — *mt*
Mostly 5–11 (–15.5) μm in length — *am*
Mostly 5–12.5 (–19) μm in length — *re, st*
Mostly 7–21 μm and when irregular reaching 35 μm in length — *se*

X. Chlamydospores:
A. Present — *aa, ad, at, ca, ho, mm, ma, mc, mo, mr, mt, ni, sc*
B. Absent — *am, re, se, st*

XI. Giant cells:
A. Present — *am, se*
B. Absent — *aa, ad, at, ca, ho, mm, ma, mc, mo, mr, mt, ni, re, sc, st*

ZYGOSPORIC STATE

I. Discovery:
   A. Found – *am, ho, mm, mc, mr, re, se, st*
   B. Not yet found – *aa, ad, at, ca, ma, mo, mt, ni, sc*

II. Type of sexual reproduction:
   A. Heterothallic — *mm, mc, mr, re, st*
   B. Homothallic — *am, ho, se*

III. Zygosporangia:
   A. Formation:
      Formed — *am, ho, mm, mc, mr, re, se, st*
      Not formed — *aa, ad, at, ca, ma, mo, mt, ni, sc*
   B. Diameter:
      Reaching 55 µm or more — *mr*
      Reaching 65 µm or more — *mc*
      Reaching 90 µm or more — *mm*
      Reaching 100 µm or more — *ho*
      Reaching 150 µm or more — *re*
      Reaching 160 µm or more — *se*
      Reaching 200 µm or more — *st*
      Reaching 230 µm or more — *am*
   C. Colour:
      Black – *se*
      Dark brown – *am, mm, mc, mr, re, st*
      Brown to yellowish brown – *ho*

IV. Azygosporangia:
   A. Formation:
      Formed — *am, ma, se*
      Not formed — *aa, ad, at, ca, ho, mm, mc, mo, mr, mt, ni, re, sc, st*
   B. Diameter:
      Reaching 60 µm or more — *ma*
      Reaching 170 µm or more — *se*
      Reaching 180 µm or more — *am*
   C. Colour:
      Black — *se*
      Dark brown — *am*
      Brown to dark brown — *ma*

V. Zygospores:
   A. Formation:
      Formed — *am, ho, mm, ma, mc, mr, re, se, st*
      Not formed — *aa, ad, at, ca, mo, mt, ni, sc*
   B. Diameter:
      Reaching 50 µm or more — *ma, mr*
      Reaching 60 µm or more — *mc*

Reaching 80 μm or more — *mm*
Reaching 100 μm or more — *ho, re*
Reaching 150 μm or more — *se, st*
Reaching 200 μm or more — *am*

C. Presence of a large oil globule:
Present — *ho, mm, ma, mc, mr*
Absent — *am, re, se, st*

D. Outer wall:
Verrucose — *am, ho, re, st*
Crenulate — *mm, ma, mc, mr, se*

D. Colour:
Hyaline — *ho, mm, ma, mc, mr, re, st*
Pale greenish — *am*
Pale brownish — *se*

VI. Suspensors:

A. Number per zygosporangium or azygosporangium:
Two — *am, ho, mm, mc, mr, re, se, st*
One — *ma*

B. Equality of the two suspensors supporting a zygosporangium:
Equal in shape and size — *am, re, se, st*
Equal in shape but unequal in size — *ho*
Unequal in shape and size — *mm, mc, mr*

C. Diameter:
Larger suspensors:
Reaching 30 μm or more — *ma*
Reaching 40 μm or more — *mm, mc, mr*
Reaching 60 μm or more — *ho*
Reaching 90 μm or more — *re, se*
Reaching 110 μm or more — *st*
Reaching 160 μm or more — *am*
Smaller suspensors:
Reaching 10 μm or more — *mr*
Reaching 20 μm or more — *mm, mc*
Reaching 40 μm — *ho*
Same as the larger suspensors — *am, re, se, st*

D. Septation:
Absent — *am, ho, mm, ma, mc, mr*
Mostly absent, rarely 1(-2) — *re, se, st*

E. Shape:
Larger suspensors:
Globose to subglobose – *am, ho*
Ovoid to subglobose – *mm, mc, mr, se*
Irregular – *ma*
Gradually widening upwards – *re, st*

Smaller suspensors:
Slightly inflated to not inflated and straight — *mm, mc, mr*
Same as the larger suspensors — *am, ho, re, se, st*

F. Constriction:
Larger suspensors:
Constricted — *am, ho, mm, ma, mc, mr, re, se, st*
Not constricted — *none*
Smaller suspensors:
Constricted or not constricted — *am, ho, mm, mc, mr, re, se, st*
Other conditions — *none*

G. Incrustation:
Incrusted — *am, mm, ma, mc, mr, re, se*
Rarely incrusted — *st*
Not incrusted — *ho*

H. Colour:
Brownish — *am, ma, mc, mr, re, st*
Brownish to orange-brown — *ho, mm, se*

NON-MORPHOLOGICAL CHARACTERISTICS

I. Maximum growth temperature:
A. 26–27 °C — *am, se*
B. 30–33 °C — *re, st*
C. 38–42 °C — *aa, ad, at*
D. 40–41 °C — *mt, ni*
E. 42–43 °C — *ho*
F. 44–49 °C — *ca, mm, mc, mo, sc*
G. 46–51 °C — *ma, mr*

II. DNA length (bp) of respectively entire ITS region (including 5.8S) and *pyrG* gene intron 1 & intron 2:
A. 450, 66, 63 — *sc*
B. 535-541, 56, 58 — *aa, ad, at, ni*
C. 538, 61, 0 — *am*
D. 553, 47, 59 — *ho*
E. 561, 53, 71 — *ca*
F. 604-606, 62-67, 53-55 — *mm*
G. 606-607, 56-60, 50-53 — *ma, mo, mt*
H. 606-608, introns 1 & 2 not tested — *mc, mr*
I. 656-658, 46, 56 — *re*
J. 734, 63, 0 — *se*
K. 788, 82, 0 — *st*

Dichotomous Key

1. Rhizoids always present, well developed, very abundant and rhizopodiformis; sporangiophores mostly reaching 2 (–4) mm in length; sporangiospores usually with distinct striation; chlamydospores absent in almost all strains; giant cells present or absent; zygosporangia dark brown to nearly black, reaching 150 (–230) μm diam.; suspensors equal in shape and size; maximum growth temperature not exceeding 33 °C 2
1. Rhizoids present or absent, generally not developed so well and less abundant, rhizopodiformis, finger-like when present; sporangiophores never exceeding 2.5 mm in length; sporangiospores with or without striation; chlamydospores easily found on mycelia; giant cells absent; zygosporangia brown or reddish brown, smaller in diameter; suspensors equal or unequal in shape and generally unequal in size; maximum growth temperature exceeding 33 °C . 5
2. Giant cells present in mycelia; sporangia not exceeding 200 μm diam.; both zygosporangia and azygosporangia present; zygospores faintly coloured; suspensors abruptly enlarging into a globose shape; homothallic 3
2. Giant cells absent in mycelia; sporangia may exceeding 200 μm diam.; zygosporangia present and azygosporangia absent; zygospores hyaline; suspensors slowly enlarging and never globose in shape; heterothallic 4
3. Colonies 1–2 mm high on L-PDA at 20 °C; sporangiophores 340–1500 (–1900) μm long and 11–19 (–26) μm diam., always simple, 1–3 in groups; striation of sporangiospores indistinct; zygosporangia 72–236 μm diam.; zygospores typically pale greenish; suspensors 54–164 μm diam.; azygospores rare . . . . *R. americanus*
3. Colonies 4–7 mm high on L-PDA at 20 °C; sporangiophores (260–) 1200–2100 (–2770) μm long and (10–) 18.5–32 (–41) μm diam., simple, sometimes dichotomously branching 1–2 times, very rarely verticillate, 1–8 in groups; striation of sporangiospores distinct; zygosporangia 64–164 μm diam.; zygospores typically pale brownish; suspensors 47–94 μm diam.; azygospores abundant . . . . . *R. sexualis*
4. Rhizoids profuse, repeatedly branching many times; sporangiophores reaching 2700 (–4000) μm in length; sporangia not nodding; zygospores with moderately dense and pointed projections; suspensors smooth and hyaline . . . . . *R. stolonifer*
4. Rhizoids less profuse, repeatedly branching 1-several times; sporangiophores reaching 1400 (–2900) μm in length; a small to large portion of sporangia nodding; zygospores with dense and pointed projections; suspensors heavily incrusted and brown . . . . . *R. reflexus*

5. Rhizoids usually branching when present; sporangiophores often reaching 1.5 mm in length; sporangiospores with visible striation; zygosporangia brown, reaching 140 μm but not exceeding 180 μm diam.; suspensors equal or unequal (fide Schipper, 1984); maximum growth temperature reaching 42 °C 6
5. Rhizoids usually finger-like when present; sporangiophores often not exceeding 1 mm in length; sporangiospores without or with faint striation; zygosporangia reddish brown, reaching 55 μm and not exceeding 120 μm diam.; suspensors equal or unequal in shape, always unequal in size; maximum growth temperature reaching 51 °C 8
6. Swellings on sporangiophores common, usually at the upper-half portion and typically just beneath the apophysis; sporangiospores variable in shape and size, (4.5–) 5.0–14.5 (–23) μm or more in length . . . . . *R. arrhizus* var. *delemar*
6. Swellings on sporangiophores less common, mostly at the middle portion when present, seldom just beneath the apophysis; sporangiospores uniform in shape and size, (4.5–) 5.0–8.0 (–9.0) μm in length 7
7. Rhizoids usually present and better developed, finger-like or branched; sporangiophores mostly arising from stolons and opposite rhizoids, brown to dark brown coloured, often exceeding 1000 μm in length; columellae regular ovoid to broad ovoid, or globose, typically with a narrow base in the larger ones, roundish conical to subglobose in the smaller ones . . . . . *R. arrhizus* var. *tonkinensis*
7. Rhizoids usually absent or poorly developed, simple or seldom branched; sporangiophores mostly arising from mycelia or from stolons with or without opposite rhizoids, yellowish brown or light brown, mostly not exceeding 1000 μm in length; columellae mainly subglobose, hemiglobose to roundish conical, very rarely oblong-ovoid, with a wide base . . . . . *R. arrhizus* var. *arrhizus*
8. Sporangiophores solitary or less than 5 in a group 9
8. Sporangiophores solitary or 2–10 in a group 16
9. Colonies persistently white to slightly yellowish; aerial hyphae typically twisted tightly into hyphal knots here and there; sporangiophores usually solitary, rarely 2–3 in groups . . . . . *R. niveus*
9. Colonies at first white, soon becoming gray; aerial hyphae not twisted into hyphal knots; sporangiophores solitary or 2–3 (–5) in groups 10
10. Sporangiophores mostly arising from aerial hyphae and indeterminate in length; zygosporangia and zygospores may exceeding 100 μm diam.; outer wall of zygospores distinctly verrucose; the two suspensors equal in shape but unequal in size; homothallic . . . . . *R. homothallicus*

10. Sporangiophores mostly arising from stolons and determinate in length; zygosporangia and zygospores when formed not exceeding 100 μm diam.; outer wall of zygospores crenulate and not verrucose; the two suspensors neither equal in shape nor size; heterothallic 11
11. Colonies low and only 1 mm high; stolons typically swollen and tuberose at places where rudimentary rhizoids appearing as minute to conspicuous outgrowths formed, but not swollen with normal rhizoids . . . . . *R. microsporus* var. *tuberosus*
11. Colonies 2–5 mm or reaching 8 mm high; stolons and rhizoids not as above 12
12. Sporangiophores mostly tapering upwards, simple; columellae usually globose; sporangiospores ovoid and somewhat pointed at both ends, striation evident; zygosporangia reaching 83 μm diam. . . . . *R. microsporus* var. *microsporus*
12. Sporangiophores not tapering upwards, simple or forked at the upper portion; columellae variable in shape; sporangiospores not pointed at both ends, striation faint and nearly invisible; zygosporangia when formed not exceeding 65 μm diam. 13
13. Sporangiophores non septate; azygosporangia abundant, each with one suspensor only; zygospores absent . . . . . *R. microsporus* var. *azygosporus*
13. Sporangiophores sometimes with a basal septum; azygosporangia absent; zygosporangia when formed always with two suspensors 14
14. Sporangiophores smooth; columellae very variable in shape, straight or oblique, symmetrical or asymmetrical; sporangiospores also variable, reaching 53 μm in length with the irregular ones; zygosporic state unknown . . . . . *R. microsporus* var. *oligosporus*
14. Sporangiophores smooth or minutely roughened; columellae not variable in shape, always straight and symmetrical; sporangiospores quite regular in shape and size, never exceeding 8 μm or 9 μm in length; zygosporic state already known 15
15. Rhizoids well developed and very abundant, rhizopodiformis; sporangiophores equal to subequal in width throughout, reaching 28.5 μm wide; columellae typically pyriform and reaching 105 μm high; zygosporangia usually not exceeding 55 μm diam. . . . . *R. microsporus* var. *rhizopodiformis*
15. Rhizoids not so well developed and not so abundant, finger-like; sporangiophores mostly widening upwards and reaching 18 μm wide; pyriform columellae absent, typically oblong-ovoid or globose to subglobose and not exceeding 80 μm high; zygosporangia reaching 65 μm diam. . . . . *R. microsporus* var. *chinensis*

16. On PDA colonies 2-5 mm high, white, then gray in age; sporangiophores usually simple, equal in width throughout, rarely widening at the uppermost part, typically arising from stolons and opposite rhizoids or directly from rhizoids, nonseptate, very rarely with a basal septum; columellae without brown pigmentation . . . . . *R. caespitosus*

16. On PDA colonies less than 1 mm high, white, then vinaceous at the central portion; sporangiophores simple or formed in pairs from a common bulbous base, equal in width throughout, sometimes tapering upwards, arising from stolons and opposite rhizoids, never from rhizoids, often with 1 (–2) basal septa; columellae often with brown pigmentation at the upper portion . . . . . *R. schipperae*

Rhizopus americanus (Hesselt. & J. J. Ellis) R. Y. Zheng, G. Q. Chen & X. Y. Liu, Mycosystema 19: 473. 2000. – Figs. 1a & 1b.

≡ *Rhizopus sexualis* (G. Sm.) Callen var. *americanus* Hesselt. & J. J. Ellis, Mycologia 53: 424. 1961. (Basionym)

Colonies on PDA attaining 9 cm diam. in 3–4 days at 20 °C, low, 1–2 mm high, at first white, then dark gray, reverse dirty white. Stolons well developed, hyaline, 8–16 µm diam., smooth. Rhizoids usually present, simple and finger-like or branching many times, hyaline to light brown, sometimes septate. Sporangiophores often arising from stolons and opposite rhizoids, sometimes directly from aerial hyphae and not opposite rhizoids, solitary, or 2–3 in groups, simple and not branched, 340–1500 (–1990) µm long, 11–19 (–26) µm diam., equal throughout, rarely slightly widening upwards, smooth, straight to slightly curved, hyaline to brownish, sometimes light brown, not septate or rarely with a septum at the base. Apophyses not evident. Sporangia globose to somewhat depressed-globose, 35–117 (–153) µm diam., blackish, deliquescing immediately in water, usually leaving no collar, rarely with a small collar. Columellae ovoid or ellipsoid-ovoid, 49–83 (–129) × 36–74 (–117) µm, subglobose, 35–117 µm diam., or roundish conical, 16–74 × 21–82 µm, hyaline to pale yellowish brown. Sporangiospores ovate, subglobose or irregular, 5.5–11 (–15.5) × 5–10 (–14) µm, indistinctly angulate, faintly striate. Giant cells in substrate mycelium, not abundant, irregular in shape, 25–72 × 18–44 µm, intercalary, hyaline or with yellowish contents. Chlamydospores absent. Zygosporangia subglobose, often compressed between the suspensors, 72–236 µm diam., blackish brown when mature, with blunt, wart-like projections. Zygospores subglobose to broadly ovoid, 65–220 µm diam., with thick, prominent projections, oil glo-

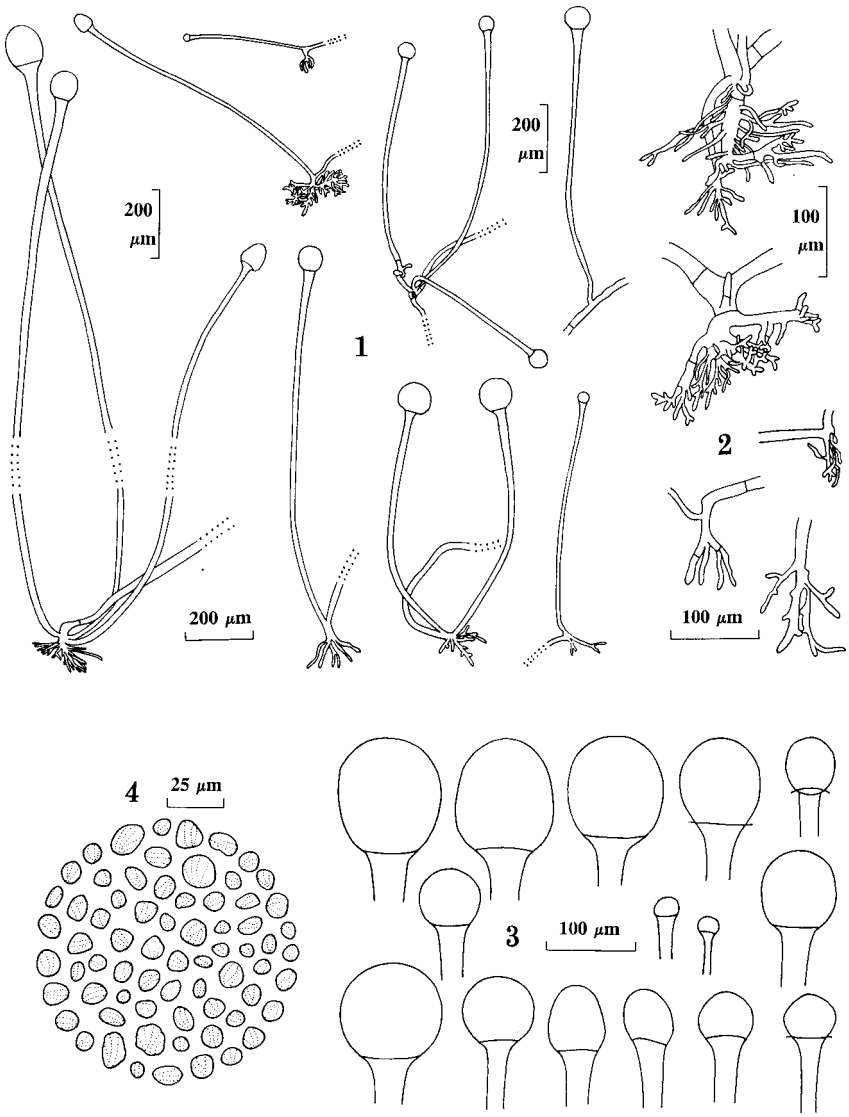

Fig. 1a. *Rhizopus americanus*. 1. General characteristics of sporangiophores. 2. Rhizoids. 3. Columellae. 4. Sporangiospores. [1–4. NRRL 2626 (= AS 3.4823), ex-Type].

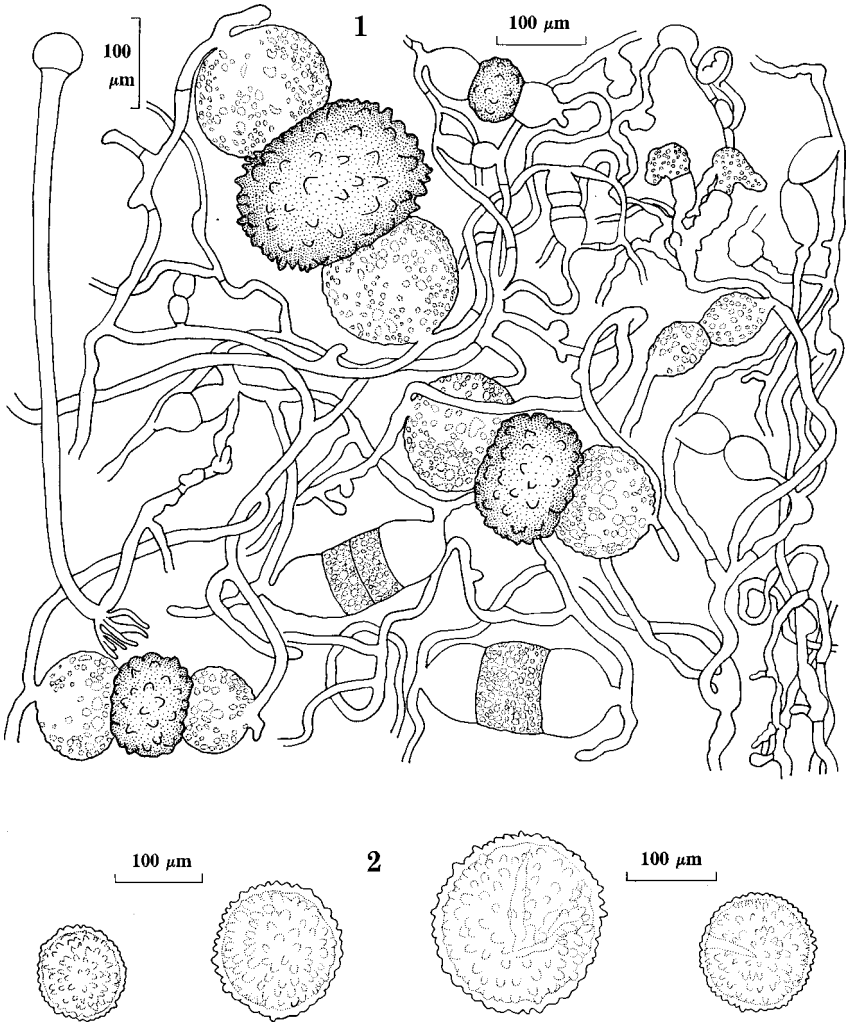

Fig. 1b. *Rhizopus americanus*. 1. Different stages and general characteristics of the zygosporic state. 2. Zygospores released from zygosporangia. [1–2. NRRL 2626 (= AS 3.4823), ex-Type].

bule absent, ridges present or absent, typically pale greenish, wall thin and easily broken. Suspensors usually equal in shape and size, always inflated, globose or subglobose, strongly constricted at the base, 54–164 μm diam., often heavily incrusted, brownish, sometimes filled with grayish-brown granules, septa generally absent. Azygosporangia formed on substrate mycelia, 70–188 μm diam. Homothallic.

Maximum growth temperature: 27 °C

DNA length of respectively entire ITS region (including 5.8S), *pyrG* gene intron 1 and intron 2: 538, 61, 0 bp.

Strain studied: **NRRL 2626** (= AS 3.4823; ±, isolated from air, Manhattan, Kansas, USA; received as, and ex-Type of *R. sexualis* var. *americanus*).

Characterization of *R. americanus:* (1) colonies are low and 1–2 mm high; (2) rhizoids are generally present, more often branching several times and with compact branches; (3) sporangiophores are 1-3 in groups, always simple, occasionally with a septum at the base; (4) sporangia are reaching 150 μm diam. and much smaller than its allied species like *R. reflexus, R. sexualis*, and *R. stolonifer;* (5) sporangiospores are with faint striation; (6) giant cells are sometimes present in the mycelia; (7) zygosporangia are the largest when compared with those of all the taxa in the same genus; (8) zygospores are typically pale greenish in colour; (9) the two suspensors supporting a zygosporangium are equal in shape and size; (10) azygospores can also be formed though not abundant. (11) sexual reproduction is homothallic.

After a comparative study on the ex-Type cultures of *Rhizopus sexualis* var. *sexualis* and *R. sexualis* var. *americanus* has been made, the latter variety was raised to species level and published as *R. americanus* stat. nov. (Zheng *et al.* 2000). The many important morphological differences of these two taxa supporting this treatment were summarized in Table 1 of that paper. DNA lengths of the entire ITS region also differ significantly in the two taxa: *R. sexualis* 734 bp, and *R. americanus* 538 bp (Liu *et al.* 2007). Maximum growth temperatures which are 26–27 °C and 27 °C, respectively, for *R. sexualis* and *R. americanus*, are almost the same.

Rhizopus arrhizus A. Fisch. *in* Rabenh., Kryptog. Fl. 1: 233. 1892. var. ***arrhizus*** – Fig. 2.

= *Amylomyces rouxii* Calmette, Ann. Inst. Pasteur 6: 611. 1892.

= *Rhizopus oryzae* Went & Prins. Geerl., Verh. Kon. Akad. Wet. Amsterdam, Sect. 2, 4: 3. 1895.

= *Chlamydomucor oryzae* Went & Prins. Geerl., Verh. Kon. Akad. Wet. Amsterdam 4: 14. 1896.

= *Chlamydomucor rouxii* (Calmette) Went & Prins. Geerl., Verh. Kon. Akad. Wet. Amsterdam 4: 16. 1896.

= *Rhizopus schizans* Mc Alpine, Fungus Diseases of Stone-fruit Trees in Australia and Their Treatment. p. 84. 1902.

= *Rhizopus tritici* Saito, Zentralbl. Bakt. ParasitKde, Abt. 2, 13: 157. 1904.

= *Rhizopus nodosus* Namysl., Bull. Acad. Sci. Cracovie 1906: 682. 1906.

= *Chlamydomucor rouxianus* (Calmette) Wehmer in Lafar, Handbuch Techn. Mykologie 4: 481. 1907.

= *Mucor norvegicus* Hagem, Unters. Norw. Mucorin. p. 39. 1908.

= *Rhizopus batatas* Nakaz., Zentralbl. Bakt. ParasitKde, Abt. 2, 24: 482. 1909.

= *Mucor nodosus* (Namysl.) Hagem, Ann. Mycol. 8: 280. 1910.

= *Rhizopus kasanensis* Hanzawa, Mycol. Centralbl. 1: 407. 1912.

= *Rhizopus trubini* Hanzawa, Mycol. Centralbl. 1: 408. 1912.

= *Rhizopus usamii* Hanzawa, Mycol. Centralbl. 1: 408. 1912.

= *Rhizopus maydis* Bruderl., Bull. Soc. Bot. Geneve, Ser. 2, 9: 108. 1917.

= *Rhizopus hangchow* M. Yamaz., J. Soc. Agric. Tokyo 185: 2. 1918.

= *Rhizopus liquifaciens* (as *'liquefaciens'*) M. Yamaz., J. Soc. Agric. Tokyo 185: 12. 1918.

= *Rhizopus albus* M. Yamaz., J. Soc Agric. Tokyo 193: 1014. 1918.

= *Chlamydomucor javanicus* M. Yamaz., J. Soc. Agric. Tokyo 201: 483. 1919.

= *Rhizopus shanghaiensis* M. Yamaz., J. Soc. Agric. Tokyo 202: 592. 1919.

= *Rhizopus peka* II Y. Takeda, Rep. Dept. Indust. Gov. Res. Inst. Formosa 5: 35. 1924.

= *Rhizopus mochi* Yosh. Yamam., 1925 (mss). (nom. inval., Art. 29.1)

= *Rhizopus fusiformis* C. O. Dawson & Povah, Science N. Y. 68: 112. 1928.

= *Rhizopus semarangensis* Y. Takeda, J. Agric. Chem. Soc. Japan 11: 907. 1935. (nom. inval., Art. 36.1)

= *Rhizopus acetoinus* Kitahara & Fukui, J. Ferm. Technol. Japan 28: 11. 1950. (nom. inval., Art. 36.1)

= *Rhizopus megasporus* Boedijn, Sydowia 12: 328.. 1958. (nom. inval., Art. 37.1)

= *Rhizopus chlamydosporus* Boedijn, Sydowia 12: 329. 1958. (nom. inval., Art. 37.1)

= *Rhizopus arrhizus* var. *rouxii* (Calmette) J. J. Ellis, Mycologia 77: 246. 1985.

Colonies on PDA attaining 9 cm diam. in 3–4 days at 27 °C, 6–10 mm high, at first white, soon becoming deep gray to black at the upper portion or in some strains the entire portion. Stolons well to poorly developed, subhyaline to brown, with or without septa. Rhizoids absent or present, finger-like or branched 1-several times when present, short to long, brownish to brown. Sporangiophores mostly arising from aerial mycelia or from stolons without opposite rhizoids, but may also from stolons with opposite rhizoids in many strains, solitary or 2–3 (–6) in groups, straight, substraight, to curved, rarely undulate or geniculate, simple, sometimes forked at the apex, (117–) 293–950 (–1740) µm long, very rarely reaching 2423 µm, mostly equal throughout, sometimes unequal at places, (7–) 9–18 (–23) µm diam., yellowish brown to brown, 0-several septate, smooth to subsmooth, sometimes subverruculose, swellings quite common, mostly at the middle portion and seldom just beneath the apophysis. Apophyses evident. Sporangia globose to sub-

globose, (47–) 71–176 (–224) µm diam., brownish black, usually slow deliquescing, mostly leaving no collar. Columellae mainly subglobose and (35–) 47–117 (–165) µm diam., hemiglobose to roundish conical and 18–97 (–117) × 37–138 (–164) µm, or ovoid to oblong-ovoid and (55–) 82–129 (–188) × (49–) 75–118 (–176) µm, often with a wide base, light brownish gray to grayish brown, mostly deeper at the upper half. Sporangiospores quite regular in shape and size, mostly ovoid, (4–) 5–8 (–9) × (3.5–) 4–7 (–8) µm, angulate, with striation, light gray when solitary, grayish brown in mass. Chlamydospores on mycelia present, in most strains not very abundant, while in strains which have abortive sporangia may become numerous, very large in size and thick-walled, intercalary and solitary or in short chains of 2–3 (–4), sometimes in small mass, oblong, ovoid, globose, to irregular, (6–) 10–37 (–66) × (5–) 10–37 (–59) µm, hyaline to yellow. Zygosporic state not found in this study, possibly heterothallic. According to Namyslowskii (1906) and Lendner (1908), zygosporangia (as 'zygospores') dark brown, average 120–140 (–180) µm diam., suspensors equal or unequal (fide Schipper 1984).

Maximum growth temperature: (37–) 39–42 °C

DNA length of respectively entire ITS region (including 5.8S), *pyrG* gene intron 1 and intron 2: 535–541, 56, 58 bp.

Strains studied: **CBS 110.17** (= AS 3.4881; from corn flour, Portugal; received as *R. oryzae*, ex-Type of *R. maydis*), **CBS 112.07** (= AS 3.4988; –, from ragi, Java, Indonesia; received as, and ex-Type of *R. oryzae*), **CBS 258.28** (= AS 3.4976 = AS 3.5053 = IFO 4809; from Chinese yeast, Hangzhou (as Hangchao or Hangchow), Zhejiang Prov., China; received as *R. oryzae*, ex-Type of *R. hangchow*), **CBS 260.28** (= AS 3.4980 = HUT 1256; from Chinese yeast, China; received as *R. oryzae,* ex-Type of *R. liquifaciens*), **CBS 264.28** (= AS 3.4990; –, from Chinese yeast, China; received as *R. oryzae,* according to Schipper (1984), ex-Type of *'R. pseudochinensis'*), **CBS 266.30** (= AS 3.4975; –, from rotten rutabaga (*Napobrassica*) in storage, USA; received as *R. oryzae*, ex-Type of *R. fusiformis*), CBS 321.35 (= AS 3.4979; from air, Russia; received as *R. oryzae*, also as *R. kasanensis* by G. Linnemann), **CBS 328.47** (= AS 3.4973; from koji, Japan; received as *R. oryzae*, ex-Type of *'R. delemar'*), **CBS 387.34** (= AS 3.4966; from koji, Japan; received as *R. oryzae*, ex-type of *R. batatas*), **CBS 395.34** (= As 3.4994; from ragi, Samarang, Indonesia; received as *R. oryzae*, ex-type of *R. semarangensis*), HUT 1219 (= AS 3.5023; from koji, Japan?; received as *R. acetoinus*), HUT 1223 (= AS 3.5024; substrate and locality unknown; received as *R. nodosus*), HUT 1227 (= AS 3.5025; substrate and locality unknown; received as *R. oryzae*, originally *R. batatas*), HUT 1250 (= AS 3.5034; substrate and locality unknown; received as *'R. japonicus'*), **HUT 1256** (= AS 3.4980 = CBS 260.28; from Chinese yeast, China; received as, and also ex-Type of *R. liquifaciens*), HUT 1257 (substrate and locality unknown; received as *'R. microsporus'*), HUT 1258 (= AS 3.5036; substrate and locality unknown; received as *R. nodosus*, originally as *R. mochi*), HUT 1275 (= AS 3.5038; substrate and locality unknown; received as *R. peka* II), **HUT 1285** (= AS 3.5039; from leaven, Shanghai, China; received as, and ex-type of *R. shanghaiensis*), **HUT 1294** (= AS 3.5052 = IFO 4798; from Chinese yeast, Shaoxing, Zhejiang Prov., China; received as, and ex-Type of *R. tritici*), IFO 4734 (= AS 3.4815; substrate and locality unknown; received as *R. oryzae*, originally *R. mochi*), IFO 4744 (= AS 3.5045; substrate and locality

unknown; received as *R. batatas*), IFO 4758 (= AS 3.5041; substrate and locality unknown; received as *'R. japonicus'*); IFO 4766 (= AS 3.5048; substrate and locality unknown; received as *R. usamii*), **IFO 4798** (= AS 3.5053 = HUT 1294; from Chinese yeast, Shaoxing, Zhejiang Prov., China; received as *R. oryzae*, ex-Type of *R. tritici*), **IFO 4809** (= AS 3.5053 = AS 3.4976 = CBS 258.28; from Chinese yeast, Hangzhou, Zhejiang Prov., China; received as, and ex-Type of *R. hangchow*), IFO 5319 (= AS 3.5054; substrate and locality unknown; received as *'R. japonicus'*, also as *'R. kansho'*), **IFO 5414** (= AS 3.4988 = CBS 112.07; from ragi, Java, Indonesia; received as, and ex-Type of *R. oryzae*), **JCM 5577** (= AS 3.4966 = CBS 387.34; from koji, Japan; received as *R. oryzae*, ex-Type of *R. batatas*), JCM 5579 (substrate and locality unknown; received as *'R. microsporus'*), **JCM 5580** (= AS 3.5570; from koji, Taiwan, China; received as *R. oryzae*, ex-Type of *R. peka* II), **JCM 5581** (= AS 3.5071; from air, Holland; received as *R. oryzae*, ex-Type of *R. nodosus*), **JCM 5584** (= AS 3.5072; from koji, Japan; received as *R. oryzae*, ex-Type of *R. usamii*), **JCM 5590** (= AS 3.5575 = AS 3.4994 = CBS 395.34; from ragi, Semarang, Indonesia; received as *R. oryzae*, ex-Type of *R. semarangensis*), **NRRL 1469** (= AS 3.5084; from rotten pod of Liliaceae, Germany; received as, and ex-Neotype of *R. arrhizus* var. *arrhizus*), NRRL 2710 (= AS 3.9514; substrate and locality unknown; received as *'R. oligosporus'*), **NRRL 3133** (= AS 3.4826 = AS 3.4988 = CBS 112.07 = IFO 5414; from ragi, Java, Indonesia; received as *R. mochi*, ex-Type of *R. oryzae*), **NRRL 5866** (= AS 3.5090; from Look Pang, Thailand; received as *R. arrhizus* var. *rouxii*, ex-Neotype of *Amylomyces rouxii*), R-55 (= AS 3.9474; from deer dung, Beijing Zoo, Beijing), R-69 (= AS 3.9475; from Chinese yeast, Sanyuan Food Products Factory, Beijing, China), R-74 (= AS 3.9993; from Chinese yeast, Beijing, China), R-141 (= AS 3. 9476; from skin lesion of a patient, Shanghai, China), R-143 (= AS 3.9477; from wheat soil, Wenxian, Gansu Prov., China), R-147 (= AS 9478; from faded flower of *Canna*, Jinghong, Yunnan Prov., China), R-152 (= AS 3.9479; from pepper soil, Xishuangbanna, Yunnan Prov., China), R-156 (= AS 3.9480; from sweet wrapping, Xishuangbanna, Yunnan Prov., China), R-158 (= AS 3.9481; from rotten leaves, Chengdu, Sichuan Prov., China), R-162 (= AS 3.9482; from fallen bamboo leaf, Chengdu, Sichuan Prov., China), R-166 (= AS 3.9483; from sweet wrapping, Anshun, Guizhou Prov., China), R-171 (= AS 3.9484 ; from pumkin soil, Dabashan, Sichuan Prov., China), R-191 (= AS 3.9485; from rotten material, Mentougou, Beijing, China), R-192 (= AS 3.9486; from rotten material, Mentougou, Beijing, China), R-195 (= AS 3.9487; from soil, Mentougou, Beijing, China), R-197 (= AS 3.9488; from soil, Mentougou, Beijing, China), R-199 (= AS 3.9489; from moldy polypore, Limushan, Hainan Prov., China), R-200 (= AS 3.9490; from moldy mushroom, Bawangling, Hainan Prov., China), R-209 (= AS 3.9491; from innerside of the bark of a dead tree, Lankao, Henan Prov., China), R-210 (= AS 3.9492; from a rotten plant, Fengjie, Sichuan Prov., China), R-211 (= AS 3.9493; from dermatosis lesion of a patient; Shijiazhuang, Hebei Prov., China), R-226 (= AS 3.9494; from mouse dung, Beijing, China), R-237 (= AS 3.9495; from Chinese yeast, Luzhou, Sichuan Prov., China), R-324 (= AS 3.9496; substrate and locality unknown, China), R-612 (= AS 3.9497; from seeds of spiceberry, Shennongjia, Hubei Prov., China), R-613 (= AS 3.9498; from Chinese yeast, Suzhou, Jiangsu Prov., China), R-712 (from the lesion of a patient of the Tongren Hospital, Beijing, China).

Characterization of *R. arrhizus* var. *arrhizus:* (1) rhizoids are usually poorly developed; (2) sporangiophores are mostly arising directly from the aerial mycelia or from stolons with or without opposite rhizoids, substraight, curved, undulate, and rarely geniculate; (3) sometimes small outgrowths can be seen at the basal part of the sporangiophores; (4) sporangiospores are comparatively small

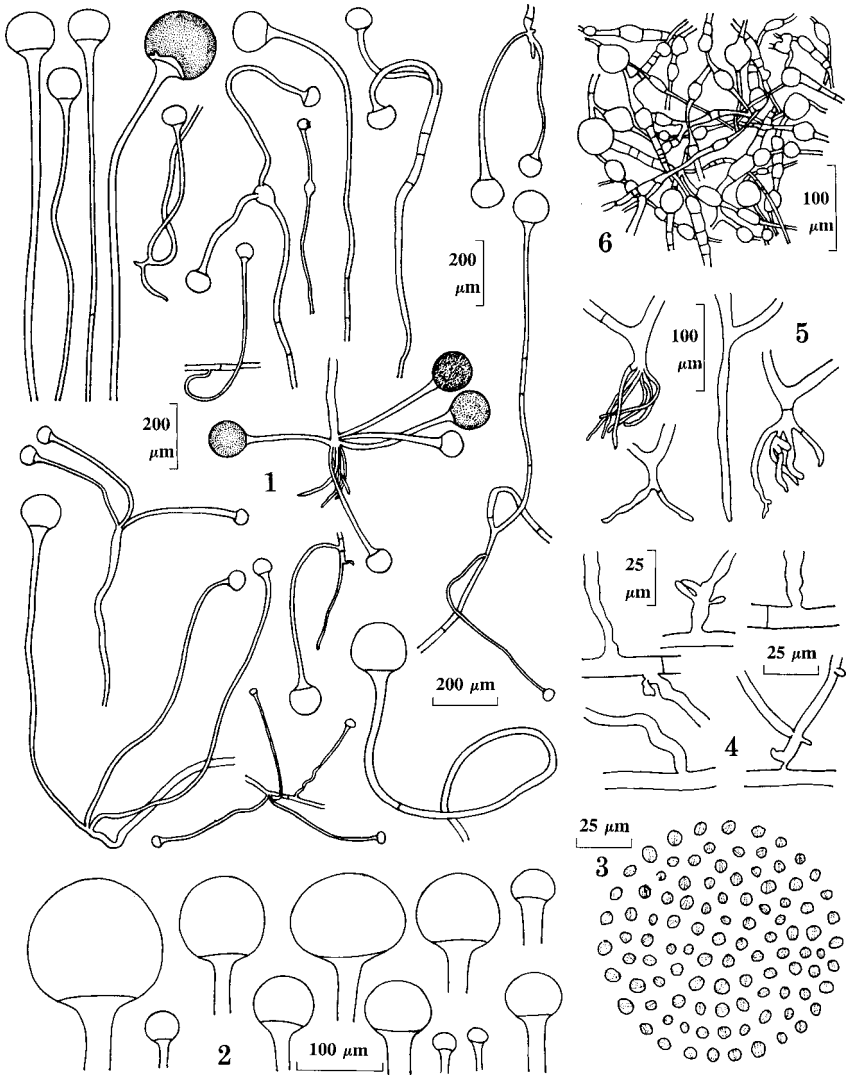

Fig. 2. Rhizopus *arrhizus* var. *arrhizus*. 1. General characteristics of sporangiophores. Note that the sporangiophores are mostly arising directly from the aerial mycelia or from stolons without opposite rhizoids. 2. Columellae which are generally subglobose, depressed globose or roundish conical. 3. Sporangiospores which are regular in shape and size. 4. Small outgrowths from the basal part of the sporangiophores. 5. Rhizoids which are simple or finger-like when present. 6. Chlamydospores. [1–6. NRRL 1469 (= AS 3.5084), ex-Neotype].

and regular in size and shape; (5) some of the long termed fermentative strains may become very degenerate, forming abortive sporangia without sporangiospores as well as abundant and very large chlamydospores.

Names of twenty-one *Rhizopus* taxa are listed as synonyms for *R. arrhizus* var. *arrhizus* in this study. Most of them are based on the examination of their ex-type cultures and at the same time the check of their diagnoses; when type cultures are not available, the remaining names can only be based on the careful study of their diagnoses.

Among the synonyms of *Rhizopus arrhizus* var. *arrhizus*, the most popular one is *R. oryzae*, but *R. arrhizus* was published three years earlier and designated with a Neotype by J. J. Ellis (1985), and should be adopted as the correct name for this fungus.

Under *Rhizopus arrhizus* Fischer, three varieties, i.e. var. *arrhizus*, var. *delemar*, and var. *rouxii*, were recognized by J. J. Ellis (1985). NRRL 5866, ex-Neotype strain of *Amylomyces rouxii* Calmette [basionym of *R. arrhizus* var. *rouxii* (Calmette) J. J. Ellis], showed 95 % relatedness when interacted with NRRL 1469, ex-Type culture of *R. arrhizus* var. *arrhizus*. Nevertheless, J. J. Ellis still retained *R. arrhizus* var. *rouxii* as a different variety according to the following reasons, " (1) it is propagated primarily by hand in association only with making fermented ragi materials, (2) it has not been isolated from nature insofar as the author can determine, and (3) strains can be readily identified on a morphological basis." In China, we have found four strains morphologically typical for *R. arrhizus* var. *rouxii*, of which, R-69 and R-613 were isolated from Chinese yeast, R-55 from deer dung, and R-612 from spiceberry seeds. Similarly, a great number of strains, either from abroad or from China, morphologically typical for *R. arrhizus* var. *arrhizus* were isolated from fermentative materials as well as from nature. In our opinion, the characteristics of *R. arrhizus* var. *rouxii*, which are, for example, the formation of abortive sporangia and the abundance of large and thick-walled chlamydospores, are the results of adaptation to fermentative environmental conditions through many generations that are retained under natural conditions. The morphology of *R. arrhizus* var. *rouxii*, is not a natural reflection of its varietal status, but a consequence of its degeneration. Results of molecular studies accomplished by our research group also showed that all strains either morphologically typical for *R. arrhizus* var. *arrhizus* or *R. arrhizus* var. *rouxii*, and either from fermentative origin or from nature, belong to the same fungus (Liu *et al.* 2008). Results of rDNA 18S, ITS, 28S sequence analyses similarly proved these two taxa to be the same fungus (Abe *et al.* 2006).

Rhizopus mochi Yosh. Yamam. was published as a provisional name in 1925, but reduced to synonymy with *R. nodosus* Namysl. in 1930 by Yamamoto himself. Three strains provided by foreign culture collections for our reference have some connexion with this fungus: HUT 1258 was labeled as *"R. nodosus*, originally *R. mochi*", IFO 4734 as *"R. oryzae*, originally *R. mochi*", and NRRL 3133 as *"R. mochi*, ex-type of *R. oryzae*". These three strains were reidentified by us to be *R. arrhizus* var. *arrhizus*. Although none of HUT 1258, IFO 4734, and NRRL 3133 is the type culture, in view of the facts that the type culture of *R. mochi* has probably been lost, and that *R. mochi* was synonymized by Yamamoto himself in 1930 with *R. nodosus* which is a synonym itself of *R. arrhizus* var. *arrhizus*, we think it appropriate to treat *R. mochi* as a synonym of *R. arrhizus* var. *arrhizus* here.

Rhizopus megasporus Boedijn and *R. chlamydosporus* Boedijn were published as 'nov. spec.' and 'nov. nom.', respectively, by Boedijn (1958). Both of them were said to be closely related to the *'R. cöhnii* Group' (*R. microsporus* Group), and characterized by their chlamydospores which are very abundant, large, and thick-walled. The diagnoses of these two taxa have clearly shown that both are not pertaining to the *R. microsporus* Group but *R. arrhizus* Group; both are synonymous with each other, and are here treated as synonyms of *R. arrhizus* var. *arrhizus*.

CBS 264.28, received as 'type of *R. pseudochinensis*', was found to be different from the real type, JCM 5585, of this name. Another strain, CBS 328.47, received as 'type of *R. delemar*', was likewise found to be different from the real type, NRRL 1472, of this name. Still another strain, JCM 5579, when received was designated as 'type of *R. microsporus*', was also found to be different from the real type of *R. microsporus*, CBS 699.68. Our identification of all these strains is *R. arrhizus* var. *arrhizus*.

Both CBS 338.62 and NRRL 2710 were received as *'R. microsporus* var. *oligosporus'* (= *R. oligosporus*) from CBS and NRRL respectively. In the study of Schipper & Stalpers (1984), these two strains were also cited as the same fungus. However, when examined by us, the original identification of CBS 338.62 was found to be correct, while NRRL 2710 was found to be a fungus morphologically intermediate between *R. arrhizus* var. *arrhizus* and *R. arrhizus* var. *tonkinensis* and not *R. oligosporus* at all. In our morphological study, most of the sporangiophores of NRRL 2710 are arising from aerial mycelia or stolons without opposite rhizoids and seldom in groups, rhizoids are usually poor or absent and hence more similar to *R. arrhizus* var. *arrhizus*; but the colour of the sporangiophores is darker and not yellowish brown, many collumellae are ovoid or oblong-ovoid and seldom hemiglobose or roundish conical, and thus some-

what similar to *R. arrhizus* var. *tonkinensis*. The final treatment of this strain is *R. arrhizus* var. *arrhizus* based on our molecular study (Liu *et al*. 2007).

Rhizopus arrhizus var. ***delemar*** (Wehmer & Hanzawa) J. J. Ellis, Mycologia 77: 247. 1985. – Fig. 3.

≡ *Rhizopus delemar* Wehmer & Hanzawa *in* Hanzawa, Mykol. Zentrbl. 1: 86. 1912. [as '(Boidin) Wehmer & Hanzawa'] (Basionym)

= *Mucor delemar* Boidin (nom. nud.)

= *Amylomyces* ß Boidin, Rev. Gen. Sci. Pures Appl. 1901: 76. 1901. (nom. inval., Art. 23)

= *Rhizopus japonicus* Vuill., Rev. Mycol. 24: 49. 1902.

= *Rhizopus formosaensis* Nakazawa, Rept. Gov. Res. Inst. Formosa 2: 37. 1913.

= *Rhizopus formosaensis* var. *chlamydosporus* M. Yamaz., J. Soc. Agric. Tokyo 185: 18. 1918.

= *Rhizopus chungkuoensis* M. Yamaz., J. Soc. Agric. Tokyo 193: 990. 1918.

= *Rhizopus salebrosus* M. Yamaz., J. Soc. Agric. Tokyo 193: 1008. 1918.

= *Rhizopus chiuniang* M. Yamaz., J. Soc. Agric. Tokyo 202: 576. 1919.

= *Rhizopus thermosus* Yosh. Yamam., J. Soc. Agric. Forest., Sapporo 17: 85. 1925.

= *Rhizopus acidus* Yosh. Yamam., J. Soc. Agr. Forest., Sapporo 17: 97. 1925.

= *Rhizopus achlamydosporus* Y. Takeda, J. Agric. Chem. Soc. Japan 11: 905. 1935. (nom. inval., Art. 36.1)

= *Rhizopus chungkuoensis* var. *isofermentarius* Y. Takeda, J. Agric. Chem. Soc. Japan 11: 907. 1935. (nom. inval., Art. 36.1)

= *Rhizopus bahrnensis* Y. Takeda, J. Agric. Chem. Soc. Japan 11: 908. 1935. (nom. inval., Art. 36.1)

= *Rhizopus javanicus* Y. Takeda, J. Agric. Chem. Soc. Japan 11: 909. 1935. (nom. inval., Art. 36.1)

= *Rhizopus delemar* var. *minimus* Y. Takeda, J. Agric. Chem. Soc. Japan 11: 910. 1935. (nom. inval., Art. 36.1)

= *Rhizopus oryzae* var. *araneosus* Y. Takeda, J. Agric. Chem. Soc. Japan 11: 911. 1935. (nom. inval., Art. 36.1)

= *Rhizopus septatus* S. F. Fang, Ann. Soc. Sci. Bruxelles, Sér. II, 57: 117. 1937.

= *Rhizopus sontii* Reddi & Subrahm., Trop. Agr. 14: 312.. 1937. (nom. inval., Art. 34.1)

= *Rhizopus javanicus* var. *kawasakiensis* Y. Takeda & A. Takamatsu, J. Agric. Chem. Soc. Japan 23: 74. 1949. (nom. inval., Art. 36.1)

= *Rhizopus delemar* var. *multiplicisporus* Inui, Y. Takeda & Iizuka, J. Gen. Appl. Microbiol., Suppl 11: 93. 1965.

Colonies on PDA attaining 9 cm diam. in 3–4 days at 27 °C, 6–10 mm high, at first white, soon becoming deep gray to black at the upper portion or the entire portion. Stolons well developed, sometimes undulate, subhyaline to brown, with or without septa, sometimes minutely roughened or with small protuberances. Rhizoids absent or present, finger-like or branched 1-several times when present, short to long, grayish-brown to brown. Sporangiophores mostly arising from stolons with opposite rhizoids or sometimes directly from mycelia and without rhizoids, solitary or 2–3 (–6) or

very rarely reaching 12 in groups, straight, substraight to curved, sometimes undulate at the lower portion or geniculate at the middle portion, simple, sometimes forked or trifurcate at the apex, (140–) 282–988 (–1552) µm long, very rarely reaching 2034 µm, equal throughout or slightly enlarging at the uppermost part, (7–) 9–20 (–27) µm diam., yellowish brown to brown, not septate, smooth to verruculose, swellings common, often at the upper half, and typically just beneath the apophysis. Apophyses evident. Sporangia globose to subglobose, (47–) 68–176 (–235) µm diam., usually quickly but sometimes slowly deliquescing, mostly not leaving a collar. Columellae ovoid to oblong-ovoid and (47–) 82.5–153 (–188) × (41–) 76.5–141 (–176) µm, broad-ovoid to subglobose and (18–) 47–106 (–153) µm diam., roundish-conical or rarely hemispherical and (18–) 35.5–94 (–118) × (27–) 53–106 (–153) µm, with a wide base, light to deep yellowish-brown, grayish-brown in the smaller ones, deeper at the upper half. Sporangiospores irregular in shape and size, ovoid when regular in shape, (4–) 5.5–14.5 (–23, reaching 52) × (3.5–) 4–8 (–13.5) µm, slightly angulate, with distinct striation, grayish when solitary, grayish brown in mass. Chlamydospores on mycelia present in almost all strains, but usually not very abundant, intercalary, generally solitary, sometimes in mass, on sporangiophores often solitary and formed just beneath the apophysis, or located at the middle part, globose and 9–41 µm diam., or oblong, ovoid to irregular, and (9–) 14–60 (–141) × (7–) 9–32 (–55) µm, hyaline to yellow. Zygosporic state unknown, probably heterothallic.

Maximum growth temperature: (38–) 40–41 °C

DNA length of respectively entire ITS region (including 5.8S), *pyrG* gene intron 1 and intron 2: 535-541, 56, 58 bp.

Strain studied: **CBS 279.38** (= AS 3.4995; from distiller's yeast, India; received as *'R. oryzae'*, ex-Type of *R. sontii*), CBS 295.31 (= AS 3.5000; from pig, Germany; received as *'R. oryzae'*, ex-authentic culture of *'R. suinus'*, **CBS 385.34** (= AS 3.4963 = HUT 1220 = IFO 4770; from tempeh, Indonesia; received as *'R. oryzae'*, ex-Type of *R. achlamydosporus*), **CBS 386.34** (= AS 3.4965; from ragi, Tohore, Bahrn, Japan; received as *'R. oryzae'*, ex-Type of *R. bahrnensis*), **CBS 389.34** (= AS 3.4972; +, from ragi, Japan; received as *'R. oryzae'*, ex-Type of *R. 'chiuniang'* var. *isofermentarius*), **CBS 390.34** (= AS 3.4824 = HUT 1239 = IFO 4730 = NRRL 2872; from ragi, Japan; received as *'R. oryzae'*, ex-Type of *R. delemar* var. *minimus*), **CBS 391.34** (= AS 3.4977 = AS 3.5057 = IFO 5442; from ragi, Japan; received as *'R. oryzae'*, ex-Type of *R. javanicus*), **CBS 393.34** (= AS 3.4989; from distiller's yeast, Taiwan, China; received as *'R. oryzae'*, ex-Type of *'R. peka* I'), **CBS 402.51** (= AS 3.4978 = HUT 1255 = IFO 4801; from ragi, Japan; received as *'R. oryzae'*, ex-Type of *R. javanicus* var. *kawasakiensis*), **CBS 406.51** (= AS 3.5003; from ragi, Japan; received as *'R. oryzae*, possible ex-Type of *R. usamii'*), **HUT 1220** (= AS 3.4963 = AS 3.5049 = CBS 385.34 = IFO 4770; from tempeh, Indonesia; received as, and ex-Type of *R. achlamydosporus*), **HUT 1233** (= AS 3.5027; from ragi, Japan; received as, and ex-Type of *R. chiuniang*), HUT 1234 (= AS 3.5028; substrate and locality unknown; received as *'R. oryzae'*, originally as *R. chungkuoensis*), HUT 1238 (= AS 3.5030; substrate

and locality unknown; received as *'R. oryzae'*, originally as *R. delemar*), **HUT 1239** (= AS 3.4824 = CBS 390.34 = IFO 4730 = NRRL 2872), from ragi, Japan; received as, and ex-Type of *R. delemar* var. *minimus*), HUT 1243 (= AS 3.5031; substrate and locality unknown; received as *R. formosaensis*), HUT 1244 (= AS 3.5032; substrate and locality unknown; received as *R. formosaensis*), HUT 1249 (= AS 3.5033; substrate and locality unknown; received as *R. japonicus*), HUT 1252 (= AS 3.5035 = AS 3.5056 = IFO 5441); substrate and locality unknown; received as *R. javanicus*), **HUT 1255** (= AS 3.4978 = CBS 402.51 = IFO 4801; from ragi, Japan; received as, and ex-Type of *R. javanicus* var. *kawasakiensis*), **IFO 4697** (= AS 3.5040; from Chinese yeast, China; received as *R. delemar*, ex-Type of *R. chungkuoensis*), IFO 4698 (= AS 3.5041; substrate and locality unknown; received as *R. delemar*), IFO 4726 (= AS 3.5044; from brewery yeast, locality unknown (Buitenzorg?); received as *'R. oryzae'*, originally as *R. chungkuoensis* var. *isofermentarius*), **IFO 4730** (= AS 3.4824 = CBS 390.34 = HUT 1239 = NRRL 2872; from ragi, Japan; received as, and ex-Type of *R. delemar* var. *minimus*), **IFO 4735** (= AS 3.9499; from Chinese yeast, Taiwan, China; received as, and ex-Type of *R. formosaensis*), IFO 4747 (= AS 3.5046; substrate and locality unknown; received as *R. formosaensis*), **IFO 4770** (= AS 3.4963 = AS 3.5049 = CBS 385.34 = HUT 1220; from tempeh, Indonesia; received as *R. formosaensis*, ex-Type of *R. achlamydosporus*), IFO 4771 (= AS 3.4814; substrate and locality unknown; received as *R. acidus*, originally as *R. delemar*), **IFO 4801** (= AS 3.4978 = CBS 402.51 = HUT 1255; from ragi, Japan; received as *'R. oryzae'*, ex-type of *R. javanicus* var. *kawasakiensis*), IFO 5441 (= AS 3.5035 = AS 3.5056 = HUT 1252; substrate and locality unknown; received as *R. javanicus*), **IFO 5442** (= AS 3.4977 = AS 3.5057 = CBS 391.34; from ragi, Japan; received as, and ex-Type of *R. javanicus*), **JCM 5560** (= AS 3.5065 = AS 3.5085 = NRRL 1472; from ragi, Japan; received as *'R. oryzae'*, ex-Type of *R. delemar*), **JCM 5561** (= AS 3.5066; from Chinese yeast, China; received as *'R. oryzae'*, ex-Type of *R. formosaensis* var. *chlamydosporus*), **JCM 5564** (= AS 3.5067; from air, Kazan, Russia; received as *'R. trubini'*, ex-Type of *R. delemar* var. *multiplicisporus*), **NRRL 1472** (= AS 3.5065 = AS 3.5085 = JCM 5560; from ragi, Japan; received as *R. arrhizus* var. *delemar*, ex-Type of *R. delemar*), **NRRL 2872** (= AS 3.4824 = CBS 390.34 = HUT 1239 = IFO 4730; from ragi, Japan; received as *'R. oryzae'*, ex-Type of *R. delemar* var. *minimus*), R-27 (= AS 3.9500; from sugarcane soil, Hangzhou, Zhejiang Prov., China), R-28 (= AS 3.9501; from corn meal, Shennongjia, Hubei Prov., China), R-29 (= AS 3.9502; from wilted flower, Fangshan, Beijing, China), R-30 (= AS 3.9503; from broken bits of cake, Nanning, Guangxi Prov., China), R-31 (= AS 3.9504; from riverside soil, Wuming County, Guangxi Prov., China), R-33 (= As 3.9505; from fallen flower, Guilin Park, Shanghai, China), R-34 (= AS 3.9506; from plant residue, Meiling, Nanchang, Jiangxi Prov., China), R-37 (= AS 3.1136; from air, Beijing, China), R-148 (= AS 3.9507; from soil, Xishuangbanna, Yunnan Prov., China), R-149 (= AS 3.9508; from soil under a fruit tree, Xishuangbanna, Yunnan Prov., China), R-196 (= AS 3.9509; from soil, Beijing, China), R-248 (= AS 3.9510; from distiller's yeast, Dianzhou, Guangdong Prov., China), R-249 (= AS 3.9511; from distiller's yeast, Dianzhou, Guangdong Prov., China), R-540 (= AS 3.9512; from flour sauce, Beijing, China).

Characterization of *R. arrhizus* var. *delemar:* (1) sporangiophores are mostly arising from stolons with opposite rhizoids, sometimes directly from the aerial mycelia, substraight, curved, undulate, and rarely geniculate, not septate, simple, sometimes forked or trifurcate at the apex; (2) swellings are common and mainly at the upperhalf of the sporangiophores but typically just beneath the apophysis; (3) sporangiospores are irregular in size and

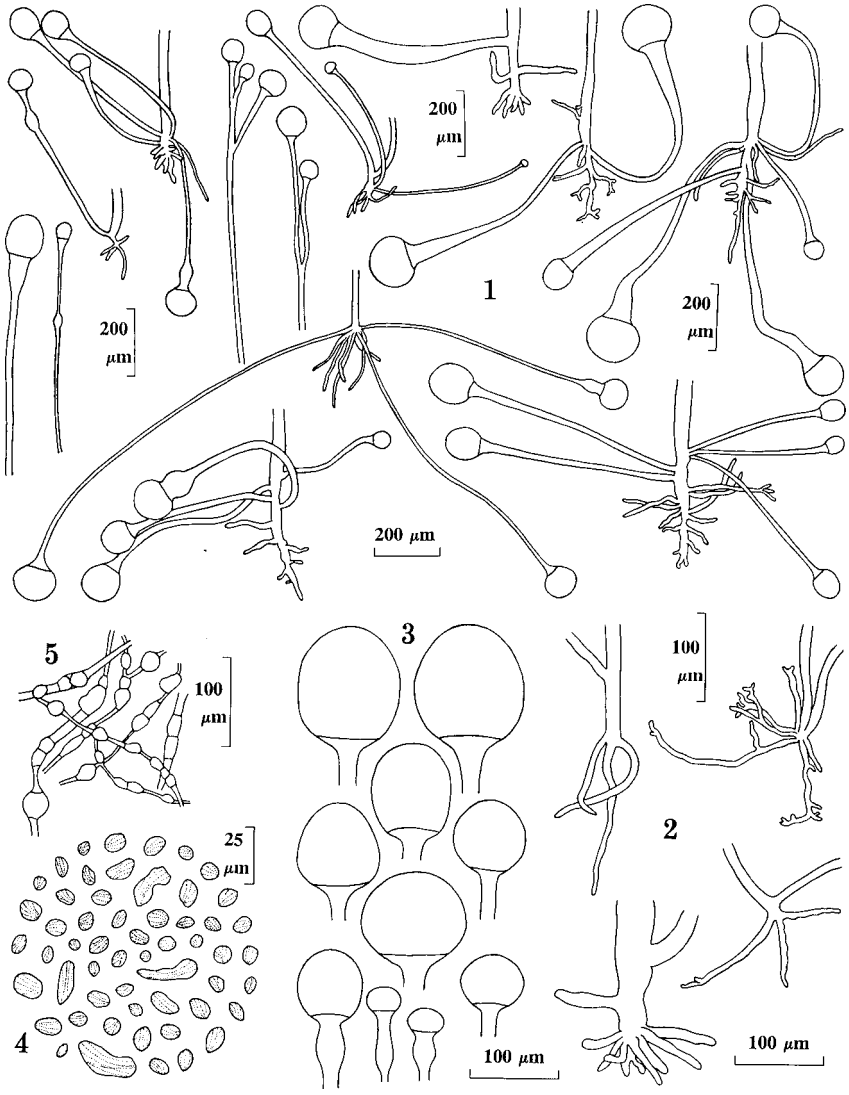

Fig. 3. *Rhizopus arrhizus* var. *delemar*. 1. General characteristics of sporangiophores. Note that the sporangiophores are mainly simple but may forked or trifurcate at the apex, mostly arising from stolons with opposite rhizoids or sometimes directly from the aerial mycelia. Also note that swellings on the sporangiophores are common and often at the upperhalf, typically just beneath the apophysis. 2. Rhizoids which are finger-like and remaining simple or branching 1(–2) times. 3. Columellae of various shapes. 4. Sporangiospores which are irregular in shape and size. 5. Chlamydospores. [1–5. NRRL 1472 (= AS 3.5065), ex-Type].

shape, and are the largest among the three varieties of the same species; (4) zygosporic state has never been reported.

When Wehmer & Hanzawa published *Rhizopus delemar* (Boidin) Wehmer & Hanzawa in the paper of Hanzawa (1912), the name they used was a combination without basionym. Instead, they provided a Latin diagnosis after the German description, and inserted the word "Diagnose:" before the name. Moreover, in the beginning of the paper, Hanzawa clearly stated that the name *Mucor delemar* was an unpublished name of Boidin which should be transferred to *Rhizopus*, and that it was a new fungus different from all known species of *Rhizopus*. Since *Mucor delemar* Boidin was a nomen nudum, it could not be used as the basionym for *R. delemar* to form a new combination. Hence, *R. delemar* (Boidin) Wehmer & Hanzawa should be considered a new species; the author name in brackets, i.e., "(Boidin)" should be deleted just like Ellis (1985) had done when he reduced *R. delemar* to varietal rank as *R. arrhizus* var. *delemar* Wehmer & Hanzawa with the basionym *R. delemar* (Wehmer & Hanzawa) Ellis. However, the pagination of *R. delemar* appeared in Hanzawa (1912) is p. 86 and not p. 77 as Ellis (1985) had cited.

In the 19 synonyms listed for *R. arrhizus* var. *delemar*, ex-Type cultures under 14 names were studied and found to be unanimous with their original descriptions and conspesific with *R. arrhizus* var. *delemar*. Ex-Type cultures of *R. japonicus, R. thermosus, R. oryzae* var. *araneosus*, and *R. septatus* were not available, but the diagnoses of them clearly show that these names are synonymous with *R. arrhizus* var. *delemar*.

The strain CBS 295.31 cited by Schipper (1984) as the type culture of *"R. suinus"* was restudied and found to be conspecific with *R. arrhizus* var. *delemar*. The diagnosis of *R. suinus* (Nielsen 1929) seems to be pertaining to a member of the *R. microsporus* Group; hence we treat *R. suinus* as a doubtful species.

CBS 389.34 was cited as "type culture of *R. chiuniang* var. *isofermentarius"* by Schipper (1984). This name has never been published, and is believed to be a misuse of the name *R. chungkuoensis* var. *isofermentarius*.

CBS 406.51 was received as "possible type culture of *R. usamii"*, when re-examined by us, it was found to be *R. arrhizus* var. *delemar* and very different from JCM 5584, the real type culture of *R. usamii*.

Rhizopus delemar was treated as a synonym of *R. oryzae* by Yamamoto (1930) and Schipper (1984), treated as a synonym of *R. oligosporus* by Kocková-Kratochvilová & Palkoska (1958), but accepted by Inui *et al.* (1965), Pidoplichko & Milko (1971), and Milko (1974). Ellis, J. J. (1985) was the first one who recognized this fungus and reduced it to varietal rank as *R. arrhizus* var. *delemar;* at the

same time, he also reduced *Amylomyces rouxii* to *R. arrhizus* var. *rouxii*. We agree with J. J. Ellis in the treatment of the former variety, but we do not accept the latter variety (see discussion under *R. arrhizus* var. *arrhizus*).

Rhizopus arrhizus var. ***tonkinensis*** (Vuill.) R. Y. Zheng & X. Y. Liu stat. & comb. nov. – Fig. 4.

≡ *Rhizopus tonkinensis* Vuill., Rev. Mycol. 24: 53. 1902. (Basionym)

= *Rhizopus tamari* Saito, Zentralbl. Bakt. ParasitKde, Abt. 2, 17: 158. 190. 1925.

= *Rhizopus boreas* Yosh. Yamam., J. Soc. Agric. Forest. Sapporo 17: 493. 1925.

= *Rhizopus kansho* Yosh. Yamam. (mss) 1925. (nom. inval., Art. 29.1)

Colonies on PDA attaining 9 cm diam. in 3–4 days at 27 °C, 6–10 mm high, at first white, soon becoming deep gray to black at the upper portion or the entire portion. Stolons present, brown to deep brown, with or without septa. Rhizoids absent or present, usually finger-like and quite long, branching at the tip, grayish brown to brown. Sporangiophores arising from stolons with or without opposite rhizoids, or directly from mycelia and without rhizoids, solitary or 2–4 (–7) in groups, substraight, but mostly curved, sometimes undulate, rarely helicoid, simple, sometimes forked or trifurcate at the apex, (118–) 306–1015 (–1739) µm long, rarely reaching 2140 µm, equal in width throughout, sometimes unequal at places, rarely enlarging at the uppermost part, (5–) 9–18 (–23) µm diam., light to deep brown, not septate, smooth to subverrucose, swellings present in some strains, sometimes giving rise to 2-3 or more branches from its upper portion. Apophyses evident. Sporangia globose to subglobose, (41–) 77–188 (–235) µm diam., quickly or slowly deliquescing, leaving no collar or a very small collar. Columellae typically and mostly strictly ovoid with a narrow base, (44–) 59–176 (–200) × (39–) 53–165 (–188) µm, others globose and (31–) 45–129 (–188) µm diam., or roundish conical and (23.5–) 35–94 (–130) × (35–) 47–106 (–141) µm in the smaller ones, yellowish or grayish brown, deeper at the upper portion. Sporangiospores regular in shape and size, mostly ovoid, (4–) 5–7.5 (–10) × (3.5–) 4–7 (–8) µm, slightly angulate, with striation, grayish when solitary, grayish brown in mass. Chlamydospores on mycelia present in many strains but usually not in large number, intercalary, generally solitary, some in short chains of 2–3 (–6), rarely in mass, globose and 7–36.5 µm diam. or oblong, ovoid to irregular and 7–36.5 (–49) × 4.5–20.5 (–44) µm, hyaline to yellow. Zygosporic state unknown, probably heterothallic.

Maximum growth temperature: (39–) 40–41 °C

DNA length of respectively entire ITS region (including 5.8S), *pyrG* gene intron 1 and intron 2: 537–540, 56, 58 bp

Strains studied: **CBS 257.28** (= AS 3.4974; from Formosan peka, Taiwan, China; received as *'R. oryzae'*, ex-Type of *'Rhizopus formosaensis'*), **CBS 330.53** (= AS 3.4967 = IFO 5318; from soil, Japan; received as *'R. oryzae'*, ex-Type of *R. boreas*), HUT 1235 (= AS 3.5029; substrate and locality unknown; received as *'R. circinans'*), IFO 4716 (= AS 3.5043, from kaoliangchiu yeast cake, locality unknown; received as *'R. oryzae'*, originally as *R. tonkinensis*), **IFO 5318** (= AS 3.4967 = CBS 330.53; from soil, Japan; received as *'R. oryzae'*, ex-Type of *R. boreas*), IFO 5384 (= AS 3.5055; substrate and locality unknown; received as *'R. oryzae'*), **IFO 5438** (= AS 3.9513; substrate and locality unknown; received as *'R. oryzae'*, ex-Type of *R. tonkinensis*), IFO 5780 (= AS 3.5058; substrate and locality unknown; received as *'R. oryzae'*, originally as *'R. arrhizus'*), **JCM 5569** (= AS 3.5068; substrate and locality unknown; received as *'R. oryzae'*, ex-Type of *R. kansho*), **JCM 5570** (= AS 3.5069; from soy koji, Japan; received as *'R. oryzae'*, ex-Type of *R. tamari*), R-42 (= AS 3.9515; from bamboo forest soil; Shennongjia, Hubei Prov., China), R-155 (= AS 3.9516; from fallen plum blossom, Jinghong, Yunnan Prov., China), R-161 (= AS 3.9517; from soil of a river bank, Chengdu, Sichuan Prov., China), R-165 (= AS 3.9518; from rotten grass, Dujianyan, Sichuan Prov., China), R-167 (= AS 3.9519; from plot soil, Longgong (?), Guizhou Prov., China), R-170 (= AS 3.9520; from eggplant soil, Tongren, Guizhou Prov., China), R-178 (= AS 3.9521; from withered twigs and fallen leaves, Yantai, Shandong Prov., China), R-180 (= AS 3.9522; from mouse dung, Beijing, China), R-183 (= AS 3.9523; from flower of hyacinth bean, Fangshan, Beijing, China), R-187 (= AS 3.9524; from soil, Mentougou, Beijing, China), R-189 (= AS 3.9525; from soil, Mentougou, Beijing, China), R-198 (= AS 3.9526; from soil, Mentougou, Beijing, China), R-205 (= AS 3.9527; from animal dung, Mutianyu, Beijing, China); R-206 (= AS 3.9528; from burnt soil, Yanqi Lake, Hebei Prov., China), R-207 (= AS 3.9529; from weeds of the lakeside, Yanqi Lake, Hebei Prov., China), R-208 (= AS 3.9530; from animal dung, Yanqi Lake, Hebei Prov., China), R-212 (= AS 3.9531; from human eye socket, Beijing, China), R-220 (= AS 3.9532; from Chinese yeast, Beijing, China; received as *R. cohnii*), R-487 (= AS 3.9533; from chestnut shell, Xiaowutai, Hebei Prov., China), R-495 (= AS 3.9534; from blue sheep dung, Jilong, Tibet, China), R-519 (= AS 3.9535; from plastic bag, Shennongjia, Hubei Prov., China), R-534 (= AS 3.9536; from soil, Hangzhou, Zhejiang Prov., China), R-710 (from air, Beijing, China), R-714 (from urine of a mucormycosis patient, Shenyang, Liaoning Prov., China).

Characterization of *R. arrhizus* var. *tonkinensis:* (1) sporangiophores are mostly arising from stolons opposite rhizoids, solitary or 2–4 (–7) in groups; (2) swellings on sporangiophores rare and usually not just beneath the apophysis; (3) columellae are typically strictly ovoid and with a narrow base, usually leaving no collar; (4) sporangiospores are regular in shape and size. (5) zygosporic state is not yet found.

Two of the strains, R-212, isolated from the eye socket of a patient of the Ophthalmology Center of the Beijing Tongren Hospital, and R-714, isolated from the urine of a patient of the hospital associated with the Shenyang Medical University, were sent to us for identification. These seem to be the first and second records for the name *Rhizopus arrhizus* var. *tonkinensis* (= *R. tonkinensis*) as a causal agent of mucormycosis.

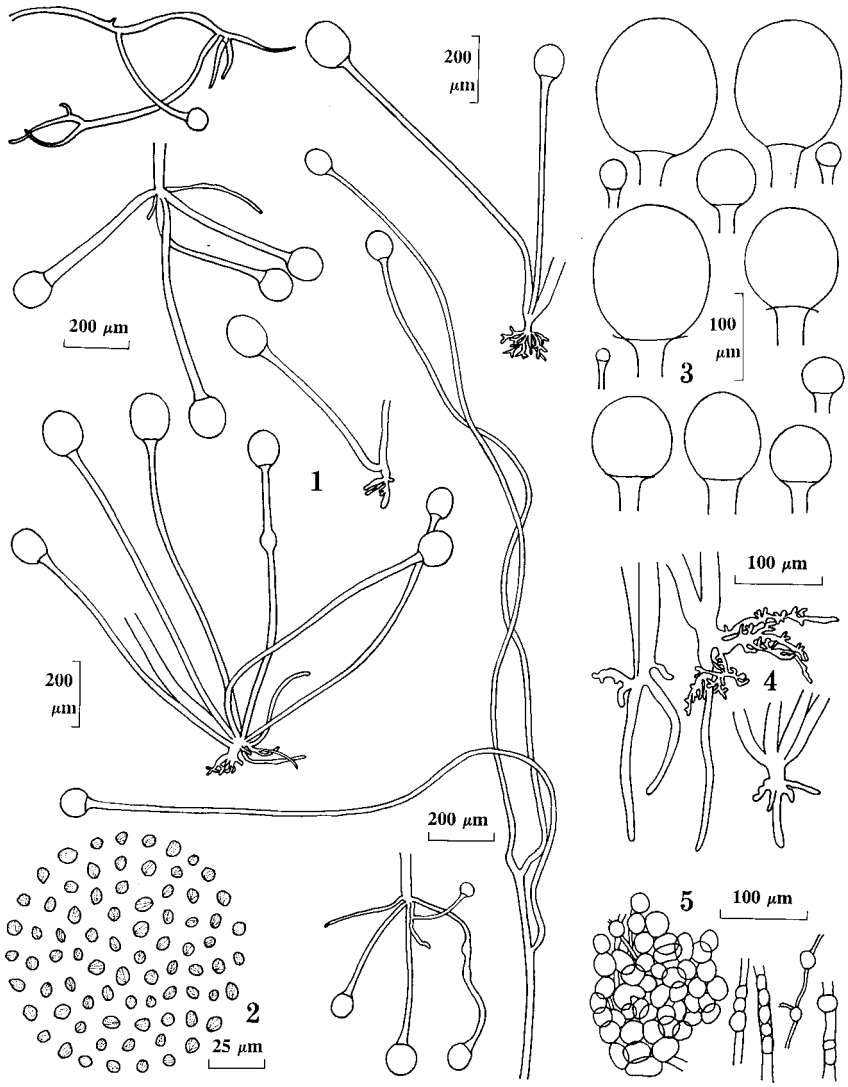

Fig. 4. *Rhizopus arrhizus* var. *tonkinensis:* 1. General characteristics of sporangiophores. Note that the sporangiophores are mostly arising from stolons with or without opposite rhizoids, sometimes from aerial mycelia and without rhizoids. 2. Sporangiospores which are regular in shape and size. 3. Columellae typically and mostly strictly ovoid, with a narrow base. 4. Rhizoids which are finger-like or branching several times. 5. Chlamydospores. [1–5. IFO 5438 (= AS 3.9513), ex-Type].

CBS 257.28 was received as the type culture of *'R. formosaensis'*, one of the synonyms of *R. arrhizus* var. *delemar*, but found to be *R. arrhizus* var. *tonkinensis* after our re-examination.

R. tonkinensis was considered to be synonymous with *R. oryzae* (*R. arrhizus* var. *arrhizus*) by most taxonomists working on the *Rhizopus* (Yamamoto 1930, Kocková-Kratochvilová & Palkoska 1958, Inui *et al.* 1965, Milko 1974, Schipper 1984), only two early works accepted this name (Lendner 1908, Naumov 1939). We also accept this name, but reducing it to a varietal rank as *R. arrhizus* var. *tonkinensis*. This treatment is supported by molecular analysis (Liu *et al.* 2008).

Rhizopus caespitosus Schipper & Samson, Mycotaxon 50: 482. 1994. – Fig. 5.

Colonies on PDA attaining 9 cm diam. in 3–4 days at 30 °C, low, 2–5 mm high, at first white, soon becoming deep gray with a greenish tint. Stolons well developed, hyaline, brownish to brown, not septate or with 1–2 septa and often swollen to 30 µm diam. at the place where rhizoids are formed. Rhizoids simple or branched, septate or not septate, usually short and robust, sometimes long and slender, subhyaline to light brown. Sporangiophores typically arising from stolons and opposite rhizoids or directly from rhizoids at the same time, solitary or 2–10 in groups, straight, substraight or bending at the base but never nodding, simple or rarely forked at the basal portion, 54–300 (–480) µm long, equal throughout or rarely widening at the uppermost part, 7.5–12.5 µm diam., thickly granular, light brown, brown, or grayish brown, sometimes paler at the tip, not septate or rarely with a septum at the base, smooth or minutely roughened. Apophyses not evident. Sporangia globose or subglobose, 37–78 µm diam., brownish black, quickly deliquescing, mostly leaving no collar. Columellae globose to subglobose, 23–59 µm diam., ellipsoid-ovoid, 23.5–55.5 × 20–50 µm, smaller ones roundish conical, 22–37 × 26.5–44 µm, smooth, granular, subhyaline to brownish. Sporangiospores regular in shape and size, mostly broadly ovoid, 5–8 (–9) × 3.5–6 (–7) µm, rarely subglobose, 4.5–7 (–8) µm diam., subsmooth, striation very faint and nearly invisible, subhyaline when single, brownish gray in mass. Chlamydospores solitary or in short chain, sometimes in mass, yellowish, 11–49 × 10–39 µm. Zygosporic state unknown, probably heterothallic.

Maximum growth temperature: 48 °C

DNA length of respectively entire ITS region (including 5.8S), *pyrG* gene intron 1 and intron 2: 561, 53, 71 bp.

Strain studied: **CBS 427.87** (= AS 3.4969; mating type unknown; substratum unknown, Naini Tal, India; received as, and ex-Type of *R. caespitosus*).

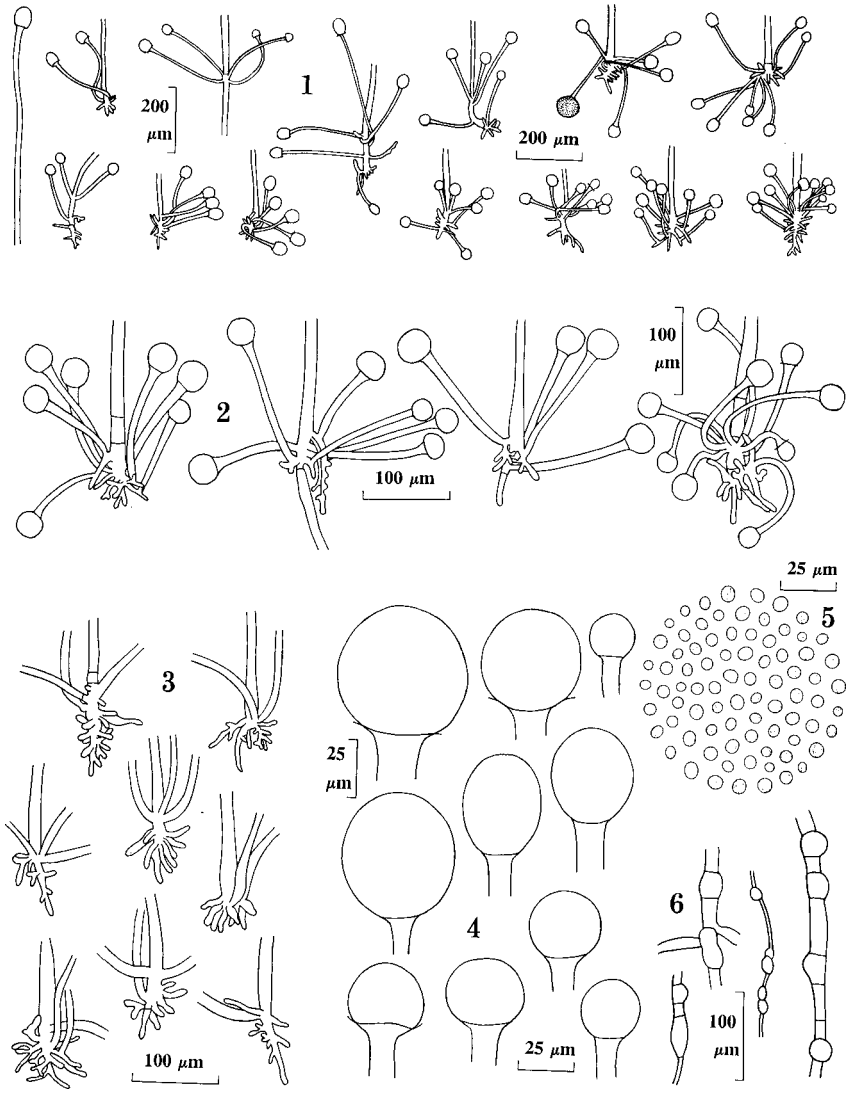

Fig. 5. *Rhizopus caespitosus*. 1. General characteristics of sporangiophores. Note that the sporangiophores may arise from aerial hyphae and without rhizoids, or arise from stolons opposite rhizoids, some of them also arise directly from rhizoids. 2. Same, with higher magnification to show the details of the sporangiophores which arise from rhizoids directly. 3. Rhizoids which are short, stout and finger-like. 4. Columellae which are ovoid or roundish, mostly without a collar. 5. Sporangiospores which are quite regular in shape and size, with very faint striation. 6. Chlamydospores. [1–6. CBS 427.87 (= AS.3.4969), ex-Type].

Characterization of *R. caespitosus:* (1) colonies are deep gray with a greenish tint; (2) rhizoids are usually short and robust, septate or not; (3) sporangiophores are typically arising from stolons and opposite rhizoids or directly from rhizoids, 1 or 2–10 in groups, equal in width throughout or rarely widening at the uppermost part, not septate or with 1 septum at the base; (4) sporangia are 37–78 μm in diameter, mostly without a collar; (5) columellae are quite regular in shape, smooth; (6) sporangiospores are also quite regular in shape and size, with faint striation; (7) zygosporic state is not yet found.

R. caespitosus has not been refound since its publication. It is also one of the very few examples in the genus that has not been reported as pathogenic to human beings or animals. CBS 427.87, the ex-Type culture of this species, did not react with any strain of the other *Rhizopus* taxa in mating experiments.

Rhizopus homothallicus Hesselt. & J. J. Ellis, Mycologia 53: 419. 1961. – Fig. 6.

Colonies on PDA reaching 9 cm diam. in 4–5 days at 30 °C, about 1 cm high, at first white, then drab gray to drab with the formation of numerous zygosporangia, reverse hair brown. Hyphae sparse. Stolons not well developed, hyaline. Rhizoids poor, usually simple and finger-like, few and short, hyaline to brownish, not septate. Sporangiophores mostly arising from hyphae and indeterminate, others arising from stolons, with or without opposite rhizoids, 212–500 (–823) μm long, mostly solitary, rarely 2 in a group, straight to substraight, sometimes curved or undulating, rarely loosely helicoid, usually simple, widening upwards, (2.5–) 9.5–19.5 (–27) μm diam., light orange-brown or light grayish brown, deeper at the upper part, becoming paler downwards, not septate, smooth. Apophyses quite evident. Sporangia globose to subglobose, 78–127 μm diam., blackish gray, deliquescing, usually without collar, sometimes with a small collar. Columellae roundish conical to depressed conical, 29–68.5 × 39–88 μm, globose or subglobose and 15–72 μm diam., oblong-ellipsoid or subovoid and 21–63.5 × 18–59 μm, mostly smooth, very rarely subverrucose at the upper portion, grayish brown. Sporangiospores regular in shape and size, subglobose or short oval, 5–8 (–9) × 4.5–7.5 μm or 4.5–8 μm diam., smooth to subsmooth, striation very faint and nearly invisible, hyaline when solitary, dark gray in mass. Chlamydospores few, solitary or in short chains, yellowish, 7–62 × 7–33 μm. Zygosporangia formed abundantly on MA4 and L-PDA media, globose or slightly depressed globose, (53–) 58.5–98 (–117.5) μm diam., brown to yellowish brown, with obtusely pointed, straight to bent projections. Zygospores globose to subglobose, similar in size, 51.5–88.5 (–110) μm diam.,

hyaline, always with a large oil globule, typically covered with many obtuse protuberances. Suspensors equal in shape but unequal in size, globose to subglobose, 39–64.5 μm and 20–39 μm diam. in the larger and smaller suspensors respectively, constricted at the base, smooth, light orange-brown or light brown. Homothallic.

Maximum growth temperature: 42–43 °C

DNA length of respectively entire ITS region (including 5.8S), *pyrG* gene intron 1 and intron 2: 553, 47, 59 bp.

Strain studied: **CBS 336.62** (= AS 3.5002; ±, from soil in a tropical desert 280 km northeast of Guatemala City, Guetemala; received as, and ex-Type of *R. homothallicus*).

Characterization of *R. homothallicus:* (1) colonies are drab gray to drab; (2) rhizoids are poorly developed or absent, not septate; (3) sporangiophores are mostly arising from hyphae and indeterminate, seldom from stolons and with or without opposite rhizoids, mostly solitary, rarely 2 in a group, widening upwards; (4) sporangia are 78–127 μm in diameter, often without a collar; (5) columellae are generally smooth but very rarely subverrucose at the upper portion; (6) sporangiospores are quite regular in shape and size with very faint striation; (7) zygospores are typically tuberculate; (8) the two suspensors are equal in shape but unequal in size, often constricted at the base; (9) sexual reproduction is homothallic.

R. homothallicus was first isolated from a soil sample collected in a very dry tropical desert of Guatemala, and several years later, a second isolate was found in India (Hesseltine & Ellis 1961). We have tried to discover this species in our country by isolating numerous soil samples collected from similar habitat but failed.

The sporangiophores of *R. homothallicus* were described as "5–30 μm and at least 2000 μm in length for those not originating opposite rhizoids", and considered to be similar to that of *R. arrhizus* by Hesseltine & J. J. Ellis (1961), but described as "up to 850 × 15 μm" by Schipper & Stalpers (1984) who included *R. homothallicus* in the *R. microsporus* Group. In our opinion, the length of the sporangiophores, when not originating from stolons, are indeterminate and unmeasurable. Furthermore, the sporangiophores of this species are widening upwards, both the diameter of the basal part and that of the upper portion should be measured. Hence, in our description for CBS 336.62, ex-Type culture of *R. homothallicus*, the sporangiophores are measured 212–500 (–823) μm in length and (2.5–) 9.5–19.5 (–27) μm in diameter, and we agree that it is a member of the *R. microsporus* Group and not near to *R. arrhizus*.

In Funindex 2000 (Anonymous 2000), *R. homothallicus* var. *indicus* B. S. Mehrotra was listed as published in 1967. A careful

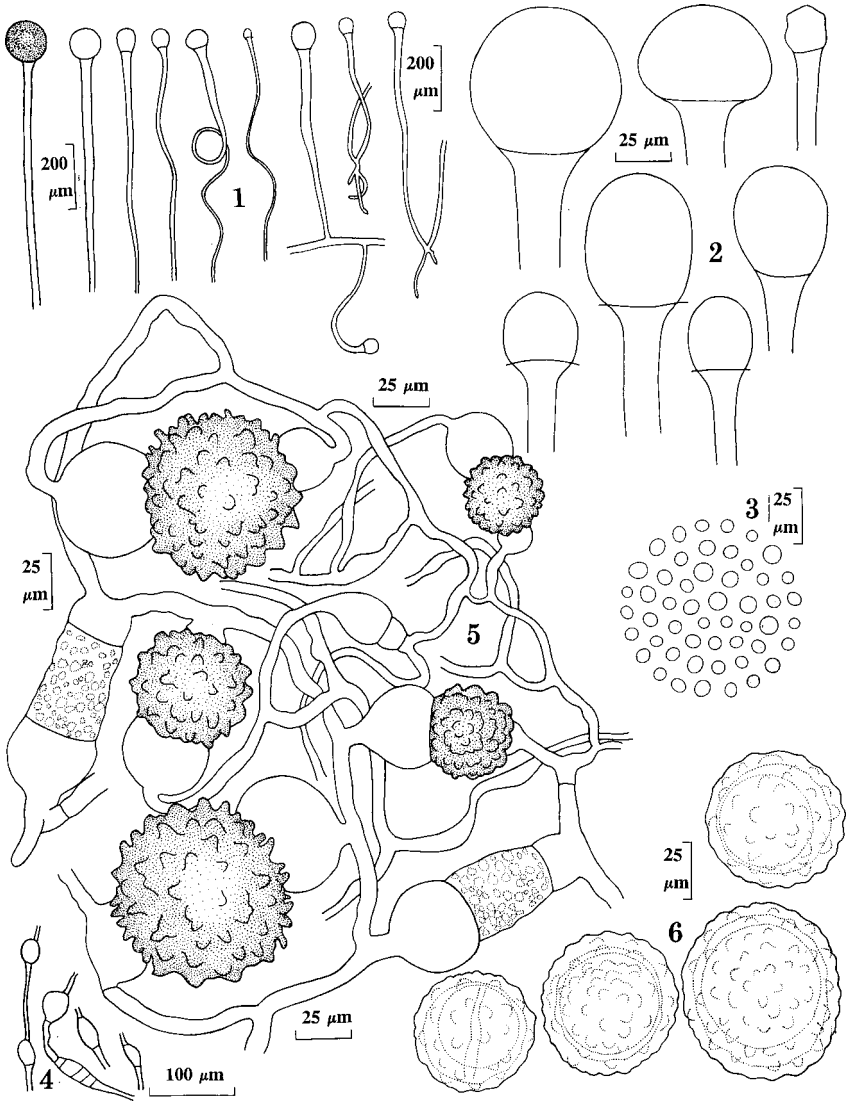

Fig. 6. *Rhizopus homothallicus*. 1. General characteristics of sporangiophores. Note that the sporangiophores are mostly arising from hyphae and indeterminate, some of them arising from stolons and with or without opposite rhizoids which are poorly developed. 2. Columellae of various shapes, usually without a collar. 3. Sporangiospores which are rather regular in shape and size, with almost invisible striation. 4. Chlamydospores. 5. Various stages of zygosporogenesis. Note that the two suspensors of a mature zygosporangium are equal in shape but unequal in size, constricted at the base, smooth and not incrusted. 6. Detached zygospores which are tuberculate. [1–6. CBS 336.62 (= AS 3.5002), ex-Type].

search in the literature could not find out where it came from. The name disappeared then in Funindex 2004 (Anonymous 2004). This name is treated as doubtful in this study.

Rhizopus microsporus Tiegh., Ann. Sci. Nat., Sér. 6, 1: 83. 1875. var. ***microsporus*** – Fig. 7.

= *Rhizopus equinus* Costantin & Lucet, Bull. Soc. Mycol. France 19: 211. 1903.

Colonies on PDA attaining 9 cm in 3–4 days at 30 °C, 2–5 (–8) mm high, at first white, soon becoming gray, brownish gray when old. Stolons when developed hyaline, brownish to brown, septate or not septate, often swollen at the place where rhizoids are formed. Rhizoids usually simple and rarely branched, short and robust, typically subequal in length, subhyaline, brownish, or grayish brown. Sporangiophores mostly arising from stolons and opposite rhizoids, solitary or 2–3 (–5) in groups, straight, substraight, or bending at the basal part, simple, 47–494 (–600) μm long, typically tapering upwards, sometimes subequal throughout, (3.5–) 5.5–10 (–13.5) μm diam., light grayish brown or light brown, sometimes paler at the tip, not septate, smooth. Apophyses shallow and inconspicuous. Sporangia globose or somewhat depressed-globose, 35–94 (–106) μm diam., at first yellowish, then brown, brownish black and black, slowly deliquescing, often leaving no collar but sometimes with a small collar. Columellae mostly globose and 23–64 (–73) μm diam., sometimes depressed globose or roundish conical and (9–) 13.5–55 (–64) × (13.5–) 19–70 (–78) μm, rarely ovoid to oblong-ovoid and (32–) 41–73 (–87) × (27.5–) 32–64 (–78) μm, smooth, light brown or light grayish brown, deeper at the upper portion. Sporangiospores quite regular in shape and size, ovoid, often somewhat pointed at both ends, 4–7 (–8) × 3–6 (–7) μm, or subglobose, 3.5–6 (–7) μm diam., smooth to subsmooth, striation evident, subhyaline or grayish when solitary, brownish gray in mass. Chlamydospores mainly solitary, sometimes in short chains, rarely in small mass, oblong, ovoid, or irregular, 7–70.5 × 4.5–41 μm, or 9–36.5 μm diam., yellow. Zygosporangia globose or subglobose, 27.5–88 μm diam., brown to deep brown, with blunt projections. Zygospores broadly oval to globose, 23.5–83.5 μm diam., outer wall thin, crenulate, usually with a large oil globule, hyaline. Suspensors unequal in shape and size, larger ones inflated, oval to subglobose, 13.5–48.5 μm diam., constricted at the base, heavily incrusted and light brownish-orange in colour, without septa, smaller ones usually not inflated or slightly inflated, 5.5–22.5 μm diam., constricted or not constricted at the base, not incrusted and hyaline, rarely light brownish-orange, without septa. Heterothallic.

Maximum growth temperature: 46–48 °C

DNA length of respectively entire ITS region (including 5.8S), *pyrG* gene intron 1 and intron 2: 604–606, 62–67, 53–55 bp.

Strains studied: **CBS 699.68** (= AS 3.4982; +, from soil, Ukrainian SSR; received as *R. microsporus* var. *microsporus*, ex-Neotype newly designated in this study), CBS 700.68 (= AS 3.4983; –, from forest soil, Georgian SSR; received as *R. microsporus* var. *microsporus*), R-39 (= AS 3.5524; from sugarcane field soil, Hangzhou, Zhejiang Prov., China), R-40 (= AS 3.5525; from soil under a pine tree, Hangzhou, Zhejiang Prov., China), R-41 (= AS 3.5526; from plant ashes, Wenling, Zhejiang Prov., China), R-43 (= AS 3.5527; from soybean field soil, Hangzhou, Zhejiang Prov., China), R-44 (= AS 3.5528; from flowerpot soil, Wenling, Zhejiang Prov., China), R-45 (= AS 3.5529; from rotten bean stalk, Wenling, Zhejiang Prov., China), R-46 (= AS 3.5530; from rotten vegetables, Wenling, Zhejiang Prov., China), R-139 (= AS 3.5531; from soil, Changsha, Hunan Prov., China), R-218 (= AS 3.2674; -, from chaff, Guiyang, Guizhou Prov., China), R-221 (= AS 3.2677; from swine dung, Beijing, China), R-222 (= AS 3.2679; from soil, Beijing, China), R-223 (= AS 3.2680; from bird's droppings, Nanjing, Jiangsu Prov., China), R-225 (= AS 3.2682; from soil, Nanchang, Jiangxi Prov., China), R-227 (= AS 3.2684; from steamed bread, Qingdao, Shandong Prov., China), R-228 (= AS 3.2685; from garden soil, Fujian Prov., China), R-229 (= AS 3.2686; from soil under a flower, Changsha, Hunan Prov., China), R-230 (= AS 3.2745; from soil, Nanchang, Jiangxi Prov., China), R-232 (= AS 3.2895; from koji, Xiamen, Fujian Prov., China), R-233 (= AS 3.3458; from barnyard manure, Nanchang, Jiangxi Prov., China), R-236 (= AS 3.3608; from koji, origin unknown), R-242 (= AS 3.5532; from garden soil, Lianyungang, Jiangsu Prov., China), R-243 (= AS 3.5533; from soil, Haikou, Hainan Prov., China), R-244 (= AS 3.5535; from fruit, Diaoluoshan, Hainan Prov., China), R-245 (= AS 3.5534; from soil, Taizhong, Taiwan Prov., China), R-712 (from the nasal cavity of a peasant, Beijing, China), R-713 (from the oral cavity, eye, and various parts of a worker of the Beijing Chemical Industry, Beijing, China).

Characterization of *R. microsporus* var. *microsporus:* (1) rhizoids are usually simple and rarely branched, short and robust, typically subequal in length; (2) sporangiophores are generally arising from stolons and opposite rhizoids, solitary or 2–3 (–5) in groups, typically tapering upwards and not septate; (3) sporangia are 35–94 (–106) µm in diameter, mostly without a collar; (4) columellae are quite regular in shape and smooth; (5) sporangiospores are often somewhat pointed at both ends and with evident striation; (6) zygospores are crenulate and never tuberculate; (7) the two suspensors are equal in shape but unequal in size, often constricted at the base; (8) sexual reproduction is heterothallic.

R. microsporus var. *microsporus* is a widely distributed species, causing various kinds of mucormycosis in human beings (Neame & Rayner 1960, Ikeda *et al.* 1987, Kerr *et al.* 1988, Udagawa 1991) and animals (Gitter & Austwick 1959). In China, this fungus was found and reported as a causal agent of mucormycosis quite late. The type culture of *R. microsporus* var. *microsporus* was lost. CBS 699.68 is designated in this study as Neotype for this fungus.

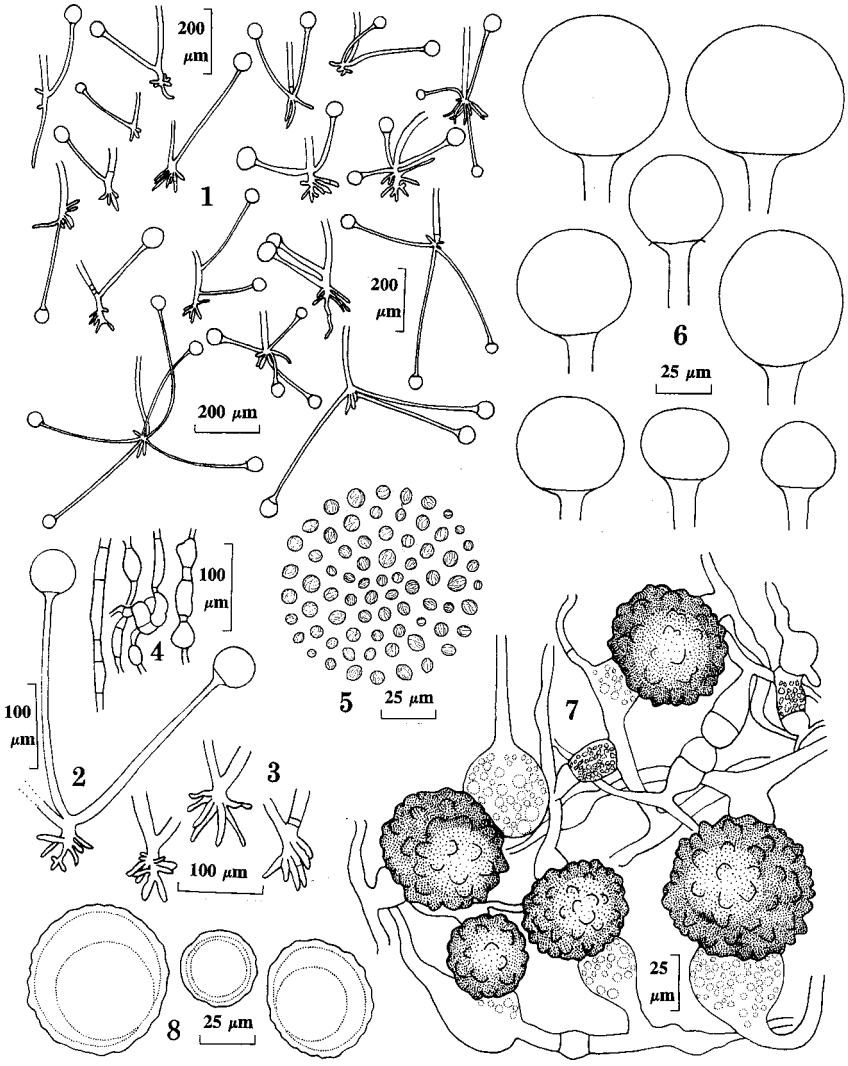

Fig. 7. *Rhizopus microsporus* var. *microsporus*. 1. General characteristics of sporangiophores. Note that the sporangiophores are usually arising from stolons opposite rhizoids and typically tapering upwards. 2. Same as 1 with higher magnification. 3. Rhizoids. 4. Chlamydospores. 5. Sporangiospores which are typically somewhat pointed at both ends and striate. 6. Columellae which are typically globose and very rarely with a small collar. 7. Various stages of zygosporogenesis. Note that the larger suspensors are oval to subglobose, heavily incrusted and constricted at the base, while the smaller ones are not, or only slightly inflated, not incrusted, constricted or not constricted at the base. 8. Detached zygospores which are crenulate and with a large oil globule. [1–6. CBS 699.68 (= AS 3.4982), ex-Neotype; 7, 8. CBS 699.68(+) × AS 3.2674(–)].

Rhizopus microsporus var. ***azygosporus*** (G. F. Yuan & S. C. Jong) R. Y. Zheng stat. & comb. nov. – Fig. 8.

≡ *Rhizopus azygosporus* G. F. Yuan & S. C. Jong, Mycotaxon 20: 398. 1984. (Basionym)

= *Rhizopus microsporus* var. *azygosporus* Schwertz, Villaume, Decaris, Percebois, & Mejean, Can. J. Microbiol. 43: 972. 1997. (nom. inval., Art. 33.2)

Colonies on PDA reaching 9 cm diam. in 3–4 days at 30 °C, 2–5 mm high, at first white, then gray, blackish gray when mature. Stolons when developed, subhyaline to light brownish gray, septate or not septate, frequently swollen at the place where rhizoids are formed. Rhizoids mostly simple, sometimes branched, very short to comparatively long, subequal in length or long and short in the same fascicle, light grayish brown. Sporangiophores mostly arising from stolons and opposite rhizoids, solitary or 2–3 (–5) in groups, straight or substraight, simple, (78–) 209–390 (–770) µm long, equal or subequal in width throughout, 8–14.5 µm diam., light to deep grayish brown, paler at the tip, not septate, smooth. Apophyses shallow. Sporangia somewhat depressed globose to subglobose, 59–107 (–127) µm diam., rapidly deliquescent, with or without collar. Columellae variable in shape, pyriform, oblong-ellipsoid, oblong-ovoid, 37–102.5 × 34–88 µm, subglobose, roundish conical, 29.5–73.5 µm diam., or broadly conical, 24.5–44 × 29.5–51 µm, mostly smooth, rarely roughened at the upper portion, often light brownish gray, a few light grayish brown, sometimes subhyaline. Sporangiospores uniform in size and shape, ovoid and 4–7 (–8) × 5–6.5 µm or subglobose and 4.5–7 (–8) µm diam., smooth, striation very faint to nearly invisible, subhyaline when solitary, dark gray in mass. Chlamydospores solitary or in short chains, sometimes in mass, oblong, ovoid, globose, or irregular, 12.5–48.5 × 8–45 µm. Azygosporangia globose or subglobose, 16.5–60 µm diam., brown to dark brown, with blunt to obtusely pointed projections. Azygospores globose to subglobose, 11.5–53 µm diam., hyaline, outer wall crenulate, with a large oil globule. Suspensors single, irregular in shape and size, often inflated, 5.5–56.5 µm long and 8.5–32.5 µm diam., mostly constricted at the base, but a few may remain straight and not constricted, not incrusted, hyaline to pale brownish. Real zygosporic state not found, probably heterothallic.

Maximum growth temperature: 49–51 °C

DNA length of respectively entire ITS region (including 5.8S), *pyrG* gene intron 1 and intron 2: 606, 58, 50 bp.

Strain studied: **CBS 357.93** (= AS 3.4964 = ATCC 48108; from tempeh, Bogor, Java, Indonesia; received as, and ex-Type of *R. azygosporus*).

Characterization of *R. microsporus* var. *azygosporus:* (1) rhizoids are mostly simple and sometimes branched, very short to compara-

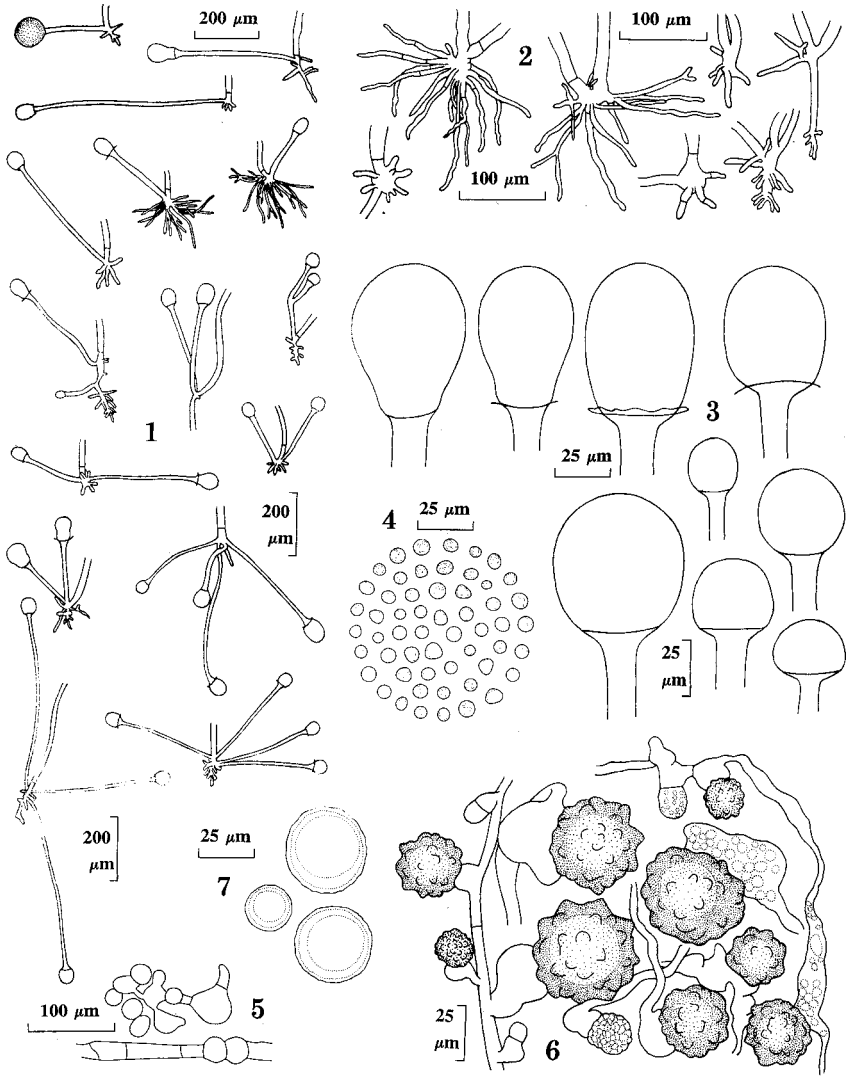

Fig. 8. *Rhizopus microsporus* var. *azygosporus*. 1. General characteristics of sporangiophores. Note that the sporangiophores are usually arising from stolons and opposite rhizoids, equal or subequal in width throughout. 2. Rhizoids. 3. Columellae of various shapes with larger ones typically pyriform, with or without a collar. 4. Sporangiospores which are quite uniform in shape and size, with very faint striation. 5. Chlamydospores. 6. Azygosporogenesis. [1–6. CBS 357.93 (= AS 3.4964), ex-Type].

tively long in length; (2) sporangiophores are generally arising from stolons and opposite rhizoids, solitary or 2–3 (–5) in groups, equal or subequal in width throughout and not septate; (3) sporangia are 59–107 (–127) μm in diameter, with or without a collar; (4) columellae are variable in shape, pyriform, oblong-ellipsoid, oblong-ovoid, subglobose or roundish conical, etc., mostly smooth but rarely roughened at the upper portion; (5) sporangiospores are quite uniform in shape and size, with very faint striation; (6) azygosporangia are often formed; (7) azygospores are not formed on MA4 but formed on PDA or L-PDA, often with a large oil-globule; (8) suspensors are single and irregular in shape and size but mostly constricted at the base; (9) true zygospores are not yet found.

The type culture of this fungus, CBS 357.93, was originally isolated from tempeh in Java as *R. oligosporus*. Yuan & Jong (1984) found azygosporangia (as "azygospores") in the fungus and published it as new species named *R. azygosporus*. We have found that, azygospores are easily formed in azygosporangia parthenogenetically when grown on PDA or L-PDA but no azygospores are formed on MA4. Except for the formation of azygosporangia, the fungus has many morphologic features in common with the varieties of *R. microsporus* and is appropriate to become an additional variety of the latter species. Molecular studies from our research group (Liu *et al*. 2008) and Abe *et al*. (2006) give strong backing to the reclassification of *R. azygosporus* as a variety of *R. microsporus*. The combination of *R. microsporus* var. *azygosporus* already used by Schwertz *et al*. (1997) is an invalid name according to Art. 33.2 of the International Code of Botanical Nomenclature (Greuter *et al*. 2000). This name is validated in this study.

Rhizopus microsporus var. ***chinensis*** (Saito) Schipper & Stalpers, Stud. Mycol. 25: 31. 1984. – Fig. 9.

≡ *Rhizopus chinensis* Saito, Zentbl. Bakt. ParasitKde, Abt. 2, 13: 156. 1904. (Basionym)

= *Rhizopus chinensis* var. *rugulosus* Hanzawa, Rept. Gov. Res. Inst. Formosa, 2: 49. 1913.

= *Rhizopus sinensis* Saito, Zentbl. Bakt. ParasitKde, Abt. 2, 13: 49. 1913.

= *Rhizopus bovinus* F. J. H. Beyma, Verh. K. Ned. Akad. Wet., Ser. C, 29: 38. 1931.

Colonies on PDA reaching 9 cm diam. in 3–4 days at 30 °C, 1–2 (–8) mm high, at first white, then gray, becoming brownish gray when old. Stolons light grayish brown to brown, septate or not septate, frequently swollen at the place where rhizoids are formed. Rhizoids usually simple, sometimes branched, short and robust, typically subequal in length, subhyaline, brownish, or grayish

brown. Sporangiophores mostly arising from stolons and opposite rhizoids, solitary or 2–3 (–5) in groups, straight, substraight, or somewhat curved at the basal part, simple or forked at the apex, (35–) 65–320 (–700) μm long, typically enlarging upwards, sometimes subequal throughout, 5.5–10 μm diam. at the base and 6.5–18.5 (–27.5) μm diam. at the upper portion, or 7–18.5 (–23) μm diam. throughout, light grayish brown, paler at the tip, without septa, very rarely with 1 basal septum, smooth or rarely minutely roughened. Apophyses quite evident. Sporangia globose or slightly depressed globose, 29.5–94 μm diam., at first yellowish, then brown, blackish brown at maturity, slowly dissolving, with or without a small collar. Columellae oblong-ovoid and (18.5–) 42–64 (–78) × (17–) 37–55 (–65.5) μm, globose or subglobose and (9.5–) 18.5–47 (–64) μm, smaller ones often roughened, roundish conical and (14.5–) 20–51.5 (–76) × (20–) 23–59 (–80) μm, light brownish gray. Sporangiospores regular in shape and size, ovoid, 5–8 (–9) × 4.5–6.5 (–7) μm, or subglobose, 4.5–7 (–8) μm diam., smooth to subsmooth, striation invisible, subhyaline to yellowish gray when solitary, brownish gray in mass. Chlamydospores abundant, solitary, in short chains, or in mass, oblong, ovoid, or irregular in shape, yellow, 7–47 (–102) × 5–37 (–60) μm. Zygosporangia globose to subglobose, 23–64.5 μm diam., at first yellowish brown, then dark brown, with blunt projections. Zygospores 20–60 μm diam., outer wall thin, slightly crenulate, usually with a large oil globule, hyaline. Suspensors unequal in shape and size, larger ones inflated, oval to subglobose, 14–41.5 μm diam., constricted at the base, smooth to subsmooth, rarely incrusted, light yellowish brown to light brown, without septa; smaller ones usually not inflated, sometimes slightly inflated, 7–21 μm diam., constricted or not constricted at the base, usually smooth and subhyaline, also without septa. Heterothallic.

Maximum growth temperature: (45–) 47–49 °C

DNA length of the entire ITS region (including 5.8S): 608 bp.

Strains studied: **CBS 294.31** (= AS 3.4968; +, from cow fetus, France; ex-Type of *R. bovinus*), **CBS 631.82** (= AS 3.4970; -, from Chinese koji, China; ex-Type of *R. chinensis*), IFO 30499 (= AS 3.5061; from rice seedling, Japan), R-36 (= AS 3.948; substrate and locality unknown, China), R-48 (= AS 3.5523; from field soil, Mongolia, China), R-214 (= AS 3.1138; substrate and locality unknown, China), R-217 (= AS 3.1166, substrate and locality unknown, China), R-224 (= AS 3.2681; from roadside soil, Hebei Prov., China), R-234 (= AS 3.4195; +, from soil, locality unknown, China), R-235 (= AS 3.4196; -, from soil, locality unknown, China).

Characterization of *R. microsporus* var. *chinensis:* (1) rhizoids are simple or branched, short and robust, typically subequal in length; (2) sporangiophores are mostly arising from stolons and opposite rhizoids, solitary or 2–3 (–5) in groups, typically enlarging

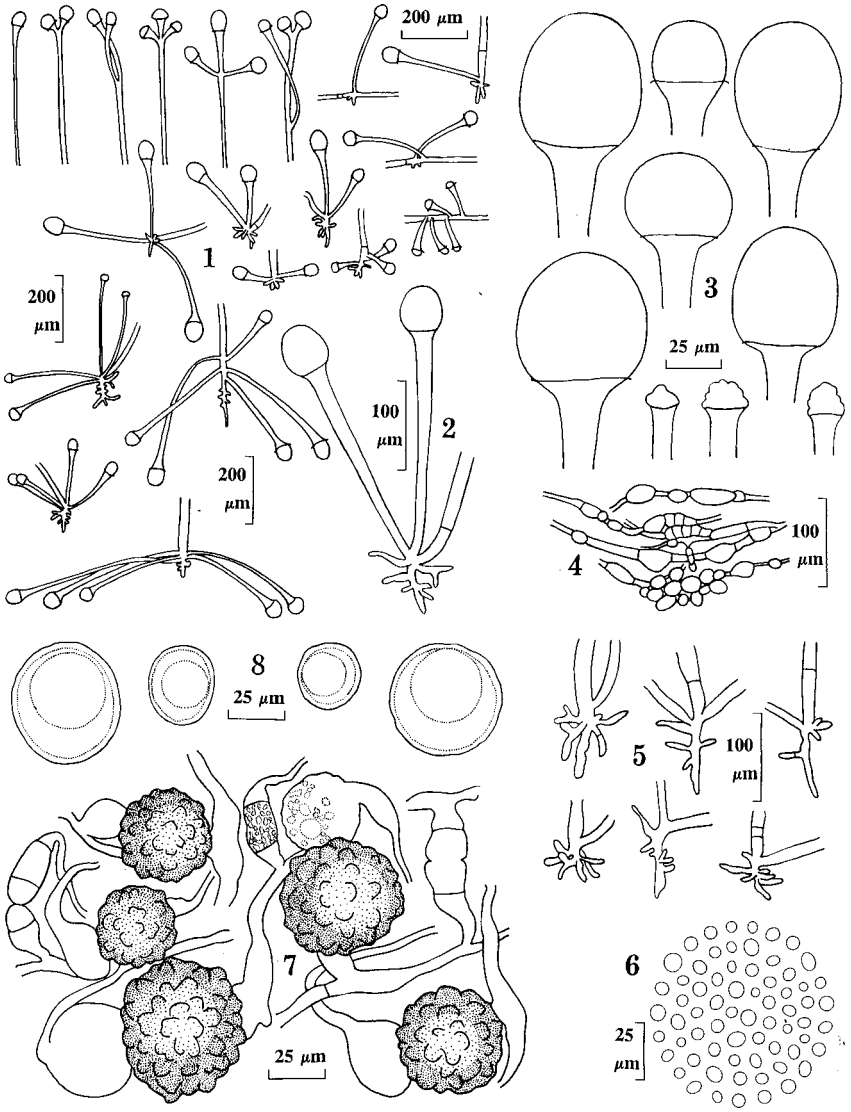

Fig. 9. *Rhizopus microsporus* var. *chinensis*. 1. General characteristics of sporangiophores. Note that the sporangiophores are arising from hyphae and indeterminate or more often from stolons and opposite rhizoids, typically widening upwards. 2. Same as 1, with higher magnification. 3. Columellae of various shapes, larger ones smooth but smaller ones usually verrucose, with or without a small collar. 4. Chlamydospores. 5. Rhizoids. 6. Sporangiospores which are quite regular in shape and size, striation invisible. 7. Various stages of zygosporogenesis. Note that the two suspensors of a mature zygosporangium are unequal in shape and size, larger suspensors oval to subglobose and constricted at the base, rarely incrusted, smaller ones usually not inflated and constricted or not constricted at the base. 8. Detached zygospores with thin outer wall and slightly crenulate. [1–6. CBS 631.82 (= AS 3.4970), ex-Type; 7, 8. CBS 294.31 (= AS 3.4968) (+) × R-235 (= AS 3.4196) (–)].

upwards, not septate or with 1 basal septum, smooth or minutely roughened; (3) sporangia are 29.5–94 μm in diameter, with or without a small collar; (4) columellae are typically oblong-ovoid, larger ones smooth, smaller ones often roughened; (5) sporangiospores are quite regular in shape and size and without striation; (6) zygospores are slightly crenulate and thin in their outer walls; (7) the two suspensors are generally unequal in shape and size, larger ones are often inflated while the smaller ones are generally not inflated; (8) sexual reproduction is heterothallic.

In earlier works, *R. microsporus* var. *chinensis* (= *R. chinensis*) has been treated quite differently by different authors: it was accepted by Lendner (1908), Yamamoto (1930), Naumov (1939), and Inui *et al.* (1965); considered to be synonymous with *R. arrhizus* by Kocková-Kratochvilová & Palkoska (1958), or with *R. cőhnii* (= *R. microsporus* var. *rhizopodiformis* or *R. rhizopodiformis*) by Pidoplichko & Milko (1971), Milko (1974), and Scholer *et al.* (1983). Later, Polonelli *et al.* (1988) proved that *R. chinensis* is intermediate between *R. microsporus* and *R. rhizopodiformis* through antigenic studies.

Rhizopus microsporus var. ***oligosporus*** (Saito) Schipper & Stalpers, Stud. Mycol. 25: 31. 1984. – Fig. 10.

≡ *Rhizopus oligosporus* Saito, Zentbl. Bakt. ParasitKde, Abt. 2, 14: 626. 1905. (Basionym)

= *Rhizopus oligosporus* var. *glaber* Nakaz., Rept. Gov. Res. Inst. Formosa, 2: 47. 1913.

= *Rhizopus peka* I Y. Takeda, Rep. Dep. Indust. Gov. Res. Inst. Formosa 5: 16. 1924.

= *Rhizopus pseudochinensis* var. *thermosus* Y. Takeda, J. Agric. Chem. Soc. Japan 11: 845. 1935. (nom. inval., Art. 36.1)

= *Rhizopus pygmaeus* Naumov, Opredelitel Mukorovych (Mucorales). 2nd rev. Edn. Bot. Inst. Acad. Sci. USSR, Moscow & Leningrad. p. 74. 1935. (nom. inval., Art. 36.1)

Colonies on PDA attaining 9 cm diam. in 3–4 days at 30 °C, (1–) 2–4 mm high, at first white, becoming gray, brownish gray when old. Stolons light grayish brown to subhyaline, with or without septa, sometimes swollen at the place where rhizoids are formed. Rhizoids usually simple, branched, often short and subequal in length, subhyaline, brownish or grayish brown. Sporangiophores mostly arising from stolons and opposite rhizoids or directly from aerial hyphae and not opposite rhizoids, solitary or 2–4 (–5) in groups, straight, substraight to curved, mostly simple, rarely forked at the apical portion, (35–) 60–294 (–500) μm long, equal in width throughout or slightly broadening upwards, (4.5–) 8.5–18 (–30) μm diam., light grayish brown, sometimes paler at the tip, usually not septate, rarely with a septum at the base, smooth. Apophyses shallow but

quite evident. Sporangia globose to somewhat depressed globose, 30–88 (–108) μm diam., at first yellowish, then brown to dark brown, almost black at maturity, slowly deliquescing, leaving no collar or a small but conspicuous collar. Columellae mostly roundish conical or depressed globose and 10–70.5 × 13–80 μm, sometimes subglobose or broadly ovoid and 15–77.5 μm diam., oblong-ellipsoid or oblong-ovoid and 22–70 × 16–64.5 μm, others very irregular in shape, straight or oblique, symmetrical or asymmetrical, light grayish brown, mostly smooth and sometimes evidently roughened in the smaller ones. Sporangiospores ovoid to subglobose, 5–9 (–14.5) × 4–11.5 μm or 4.5–9 (–11) μm diam., or very irregular in shape and much larger, 12.5–39 (–53) × 4–12.5 μm, some smooth and some subangulate, not striate, subhyaline to grayish when solitary, grayish brown in mass. Chlamydospores absent in some strains but present in the others, solitary, in short chains, or in mass, oblong, ovoid, to subglobose or irregular, yellow, 7.5–38 (–59) × 6–17 (–35) μm. Zygosporic state not found.

Maximum growth temperature: (45–) 46–48 (–49) °C

DNA length of respectively entire ITS region (including 5.8S), *pyrG* gene intron 1 and intron 2: 606-607, 56-60, 50-53 bp.

Strains studied: **CBS 337.62** (= AS 3.4984, from tempeh, Indonesia; received as *R. microsporus* var. *oligosporus*, ex-Neotype newly designated in this study), CBS 338.62 (= AS 3.4985, from tempeh, Indonesia; received as *R. microsporus* var. *oligosporus*), CBS 339.62 (= AS 3.4986, from tempeh, Indonesia; received as *R. microsporus* var. *oligosporus*), **CBS 344.29** (= AS 3.4993, substrate and locality unknown, USSR; received as *'R. microsporus* var. *chinensis'*, ex-Type of *R. pygmaeus*), **CBS 394.34** (= AS 3.4991, from ragi, Japan; ex-Type of *R. pseudochinensis* var. *thermosus*), IFO 8631 (= AS 3.4818, from tempeh, Indonesia; received as *R. oligosporus*), IFO 31987 (= AS 3.4819, substrate and locality unknown; received as *R. oligosporus*), IFO 32002 (= AS 3.4820, from tempeh, Indonesia; received as *R. oligosporus*), IFO 32003 (= AS 3.4821, from tempeh, Indonesia; received as *R. oligosporus*), **JCM 5596** (= AS 3.5076, from koji, China; received as 'Type of *R. chinensis'*), NRRL 514 (= AS 3.54984 = CBS 337.62, from tempeh, Indonesia; received as *R. oligosporus*), R-47 (= AS 3.5522, from soil, Xinjiang Prov., China), R-65 (= AS 3.5521, from human being, Shanghai, China), R-66 (from humus, Beijing, China), R-216 (= AS 3.1161, from soil, Hebei Prov., China), R-711 (from air, Beijing, China).

Characterization of *R. microsporus* var. *oligosporus:* (1) rhizoids are mostly simple but sometimes branched, often short and subequal in length; (2) sporangiophores are generally arising from stolons and opposite rhizoids, solitary or 2–4 (–5) in groups, simple or rarely forked at the apical portion, equal in width throughout or slightly broadening upwards; (3) sporangia are 30–88 (–108) μm in diameter, with or without a small collar; (4) columellae are very variable in shape, straight or oblique, symmetrical or asymmetrical, mostly smooth but sometimes evidently roughened; (5) sporangiospores are very irregular in shape and size, larger ones reach 53 μm in length,

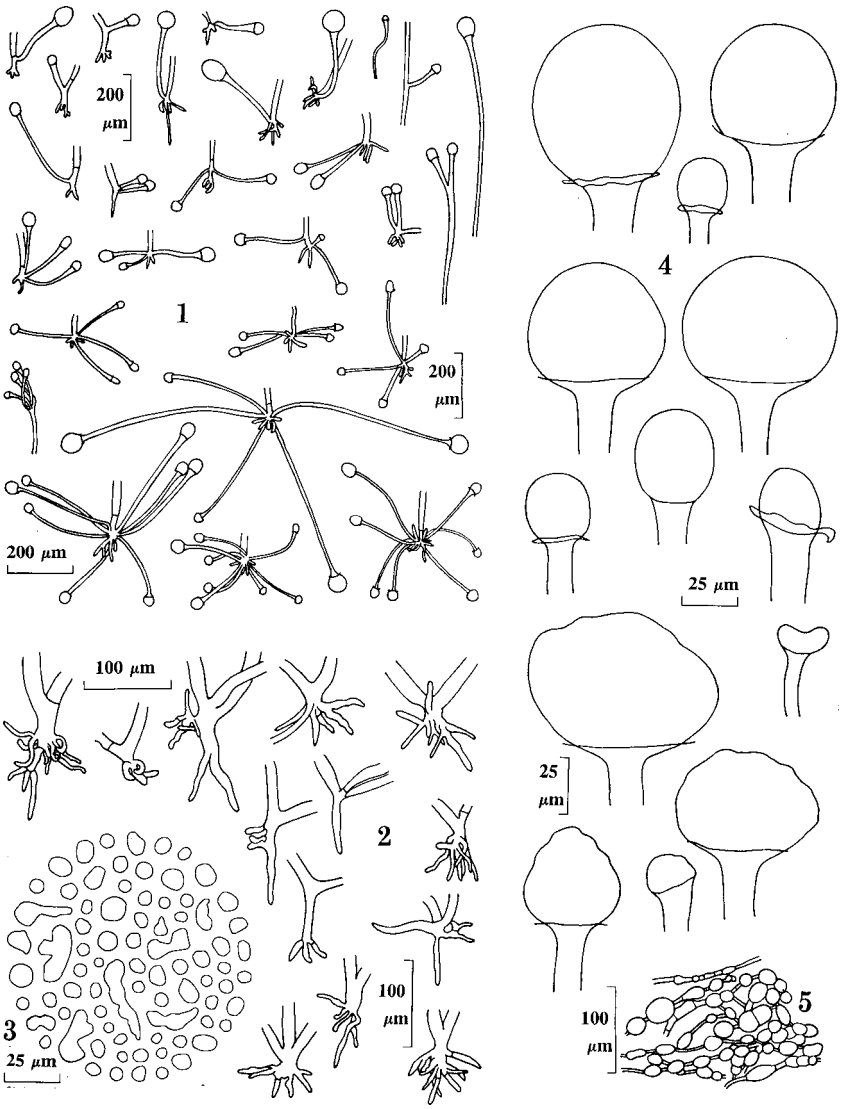

Fig. 10. *Rhizopus microsporus* var. *oligosporus*. 1. General characteristics of sporangiophores. Note that the sporangiophores are subequal in width throughout or slightly broadening upwards. 2. Rhizoids. 3. Sporangiospores which are very irregular in shape and size, not striate. 4. Columellae which are very variable in shape, with some unsymmetrical, smooth or verrucose, with or without a small collar. 5. Chlamydospores. [1–5. CBS 337.62 (= AS 3.4986), ex-Neotype].

all are not striate; (6) zygosporic state is not yet found, all mating experiments fail.

The variety is very easy to isolate from tempeh in Indonesia, and is easy to discern by its irregularly shaped columellae and spores. No zygospore was formed in numerous crossing attempts between different (+) and (–) strains of the same variety.

CBS 344.29 was identified by Schipper & Stalpers (1984) as *R. microsporus* var. *chinensis* and cited as the type culture of *R. pygmaeus*. This strain was restudied by us and found to be *R. microsporus* var. *oligosporus,* and also that the original diagnosis of *R. pygmaeus* fits *R. microsporus* var. *oligosporus* very well. Therefore, CBS 344.29 is *R. microsporus* var. *oligosporus* and not *R. microsporus* var. *chinensis,* and *R. pygmaeus* is a synonym of *R. microsporus* var. *oligosporus* and not of *R. microsporus* var. *chinensis*.

Another strain, CBS 393.34, identified by Schipper (1984) as *R. oryzae* (= *R. arrhizus* var. *arrhizus*) and cited as the type culture of *R. peka* (= *R. peka* I), was restudied by us and found to be *R. arrhizus* var. *delemar*. We have also noticed that the original diagnosis of *R. peka* I does not fit any of the *R. arrhizus* & allies, but fits *R. microsporus* var. *oligosporus* very well. Yamamoto (1930) has also pointed out that *R. peka* I might be closely related to *R. oligosporus* though he retained *R. peka* I as an independent species. Therefore, if CBS 393.34 has formerly been a real type culture of *R. peka* I, it is probably a contaminated culture of *R. arrhizus* var. *delemar* now and thus, it cannot be the type culture of *R. peka* I anymore.

Still another strain, CBS 394.34 was identified by Schipper & Stalpers (1984) as *R. microsporus* var. *chinensis* and cited as the type culture of *R. pseudochinensis* var. *thermosus*. Again, this strain was restudied by us and found to be *R. microsporus* var. *oligosporus*. We have also found that the original diagnosis of *R. pseudochinensis* var. *thermosus* fits *R. microsporus* var. *oligosporus* very well. As a result, CBS 393.34 should be *R. microsporus* var. *oligosporus* instead of *R. microsporus* var. *chinensis*. *Rhizopus pseudochinensis* var. *thermosus* could not be a synonym of *R. microsporus* var. *chinensis* but of *R. microsporus* var. *oligosporus*.

Likewise, JCM 5596 was received as, and cited as the type culture of *R. chinensis* (= *R. microsporus* var. *chinensis*). After our reexamination, it was found to be *R. microsporus* var. *oligosporus*. Most probabely JCM 5596 is a contaminated culture now and cannot represent *R. microsporus* var. *chinensis* anymore.

Before 1983, *R. microsporus* var. *oligosporus* was only known as potentially pathogenic (Scholer *et al.* 1983). Several years later, Tintelnot & Nitsche (1989) reported a mucormycosis in a patient whose fractured spinal column was infected by *R. microsporus* var. *oligo-*

sporus. In 1995, we identified the same fungus from the infected dermatosis of a patient in Shanghai.

The type culture of *R. microsporus* var. *oliosporus* was lost. CBS 337.62 is designated as the Neotype of this fungus in this study.

Rhizopus microsporus var. ***rhizopodiformis*** (Cohn) Schipper & Stalpers, Stud. Mycol. 25: 30. 1984. – Fig. 11.

≡ *Mucor rhizopodiformis* Cohn *in* Lichtheim, Z. Klin. Med. 7: 140. 1884. (Basionym)

= *Rhizopus cohnii* Berl. & De Toni *in* Sacc., Syll. Fung. 7: 213. 1888.

= *Rhizopus rhizopodiformis* (Cohn) Zopf *in* Schenk, Hand. Bot. 4: 587. 1890.

= *Rhizopus alpinus* Peyronel, I. Germi atmosfer dei Funghi con micelio. p. 17. 1913.

= *Rhizopus pseudochinensis* M. Yamaz., J. Soc. Agr. Tokyo 193: 996. 1918.

= *Rhizopus chinensis* var. *liquifaciens* (as *'liquefaciens'*) Y. Takeda, J. Agric. Chem. Soc. Japan, 11: 912. 1935. (nom. inval., Art. 36.1)

= *Rhizopus pusillus* Naumov, Opredelitel Mukorovych (Mucorales). 2nd rev. Edn. Bot. Inst. Acad. Sci. USSR, Moscow & Leningrad. p. 74. 1935. (nom. inval., Art. 36.1)

= *Rhizopus microsporus* var. *pseudochinensis* (M. Yamaz.) R. Prakash & A. K. Sarbhoy, Zentb. Mikrobiol. 148: 533. 1993.

Colonies on PDA attaining 9 cm diam. in 3–4 days at 30 °C, usually low and 1–2 (–5) mm high, rarely reaching 8 mm, at first white, soon gray, at last dark gray. Stolons hyaline to light grayish brown, septate or not septate. Rhizoids well developed, simple or branched, often subequal in length, subhyaline to grayish brown, paler at the tip. Sporangiophores mostly arising from stolons and opposite rhizoids, solitary or 2–3 (–5) in groups, straight, substraight, sometimes subcurved at the basal part, mostly simple, very rarely forked at the apex, (35–) 60–300 (–858) µm long, mostly subequal in width throughout, sometimes slightly broadening at the uppermost part, (5–) 7–18 (–23.5) µm diam., light grayish brown, paler upwards, often without septa, rarely with 1 (–2) septa at the basal part, smooth, very rarely minutely roughened. Apophyses shallow but conspicuous. Sporangia globose or somewhat depressed-globose, (24–) 41–94 (–120) µm diam., at first yellowish, then brown to dark brown, slowly deliquescing, rarely broken, leaving a small collar in most cases. Columellae typically pyriform, others oblong-ovoid or broad ellipsoid in the larger ones, (19.5–) 27–84 (–105) × (17–) 23–73 (–87) µm, roundish conical in the smaller ones, (10–) 23.5–58.5 × (12.5–) 30–78 µm, rarely subglobose, 17.5–53 µm diam., usually smooth, very rarely slightly roughened, light grayish brown, deeper at the upper portion. Sporangiospores regular in shape and size, globose to subgobose and 3.5–6 (–7) µm diam., or ovoid to subovoid and 4–7 (–8) × 3.5–7 µm, smooth to subsmooth, striation nonvisible, subhyaline to light yellowish gray when solitary,

gray to deep gray in mass. Chlamydospores present in some strains, mainly solitary, sometimes in short chains, seldom in mass, subglobose and 8.5–27.5 µm diam., or oblong, ovoid to irregular and 11.5–50 (–78) × 3.5–18.5 (–68) µm, subhyaline to yellow. Zygosporangia globose to subglobose, 23–55 µm diam., at first yellowish brown, then dark brown, with blunt projections. Zygospores globose to broadly ovoid, 20–50.5 µm diam. or 22–50 × 20–46.5 µm, outer wall thick when immature, thin and evidently crenulate when mature, usually with a large oil globule, hyaline. Suspensors unequal in shape and size, larger ones inflated, ovoid to subglobose, 13.5–46 µm diam., constricted at the base, smooth or rarely incrusted, light yellowish brown to light brown, non-septate; smaller ones usually not inflated, rarely indistinctly and slightly inflated, 3.5–12 µm diam., not constricted or slightly constricted at the base, smooth, hyaline, non-septate. Heterothallic.

Maximum growth temperature: (46–) 47–51 °C

DNA length of the entire ITS region (including 5.8S): 606 bp.

Strains studied: **CBS 343.29** (= AS 3.4992, +; from air, USSR; received as *R. microsporus* var. *rhizopodiformis,* ex-Type of *R. pusillus*), **CBS 388.34** (= AS 3.4971, –; from ragi, Indonesia; received as *'R. microsporus* var. *chinensis'*, ex-Type of *R. chinensis* var. *liquifaciens*), **CBS 536.80** (= AS 3.4987, +; from sorghum malt, South Africa; received as *R. microsporus* var. *rhizopodiformis*, ex-Neotype newly designated in this study), **HUT 1231** (= AS 3.5026; substrate and locality unknown; received as, and ex-Type of *R. chinensis* var. *liquifaciens*), **JCM 5585** (= AS 3.5073, +; from Chinese koji, China; received as, and ex-Type of *R. pseudochinensis*), R-49 (= AS 3.5540, +; from mouse dung, Wenling, Zhejiang Prov., China), R-52 (= AS 3.5539; from henhouse grasses, Wuyishan, Fujian Prov., China), R-181 (= AS 3.5538; from mouse dung, Beijing, China), R-213 (= AS 3.2746; from Chinese koji, locality unknown), R-219 (= AS 3.2675; from park soil, Guilin, Guangxi Prov., China), R-231 (= AS 3.2746, -; from cake, Hangzhou, Zhejiang Prov., China), R-238 (= AS 3.5537; from cow dung, Fuzhou, Fujian Prov., China), R-246 (= AS 3.5536; from soil, Nangang, Taipei, China).

Characterization of *R. microsporus* var *rhizopodiformis:* (1) rhizoids are well developed, often subequal in length; (2) sporangiophores are mostly arising from stolons and opposite rhizoids, solitary or 2–3 (–5) in groups, mostly subequal in width throughout, usually not septate, rarely 1–2 septate at the base; (3) sporangia are (24–) 41–94 (–120) µm in diameter, mostly with a small collar after deliquescing; (4) columellae are typically pyriform and large, reaching 105 µm in height, smooth and very rarely slightly roughened; (5) sporangiospores are regular in shape and size, with invisible striation; (6) outer walls of zygospores are thin and crenulate; (7) the two suspensors are unequal in shape and size, larger ones are inflated and constricted at the base, smaller ones are mostly not inflated and constricted or slightly constricted at the base.

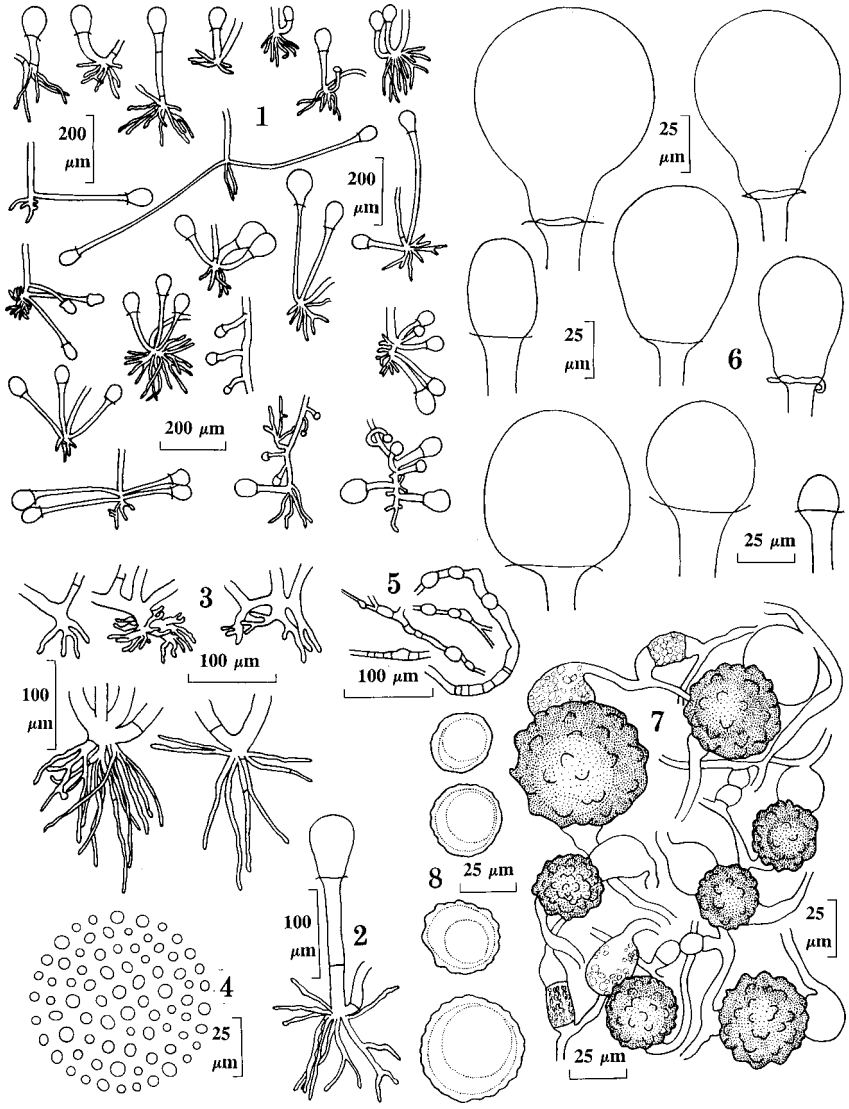

Fig. 11. *Rhizopus microsporus* var. *rhizopodiformis*. 1. General characteristics of sporangiophores. Note that the sporangiophores are mostly relatively short in length, equal in width throughout or rarely slightly broadening at the uppermost part. 2. Same as 1 with higher magnification. 3. Rhizoids which are simple or branched and well developed. 4. Sporangiospores which are not striate. 5. Chlamydospores. 6. Columellae typically pyriform and large, mostly with a small collar. 7. Various stages of zygosporogenesis. Note that the two suspensors are unequal in shape and size. 8. Detached zygospores with crenulate outer wall and a large oil globule. [1–6. CBS 536.80 (= AS 3.4987), ex-Neotype; 7, 8. R-49 (= AS 3.5540) (+) × CBS 388.34 (= AS 3.4971) (–)].

CBS 388.34 was received as *R. microsporus* var. *chinensis* and cited as the type culture of *R. chinensis* var. *liquifaciens,* and HUT 1231 was received as, and cited as the type culture of *R. chinensis* var. *liquifaciens* as well. Both CBS 388.34 and HUT 1231 were reidentified by us as *R. microsporus* var. *rhizopodiformis*. The original diagnosis of *R. chinensis* var. *liquifaciens* also agrees well to *R. microsporus* var. *rhizopodiformis*. Hence, *R. chinensis* var. *liquifaciens* should be synonymized with *R. microsporus* var. *rhizopodiformis* and not with *R. microsporus* var. *chinensis* as Schipper & Stalpers (1984) did.

R. microsporus var. *rhizopodiformis* (as *R. rhizopodiformis*) was reported to rank second in frequency after *R. arrhizus* var. *arrhizus* (as *R. oryzae*) as a pathogenic agent causing human mucormycosis and was responsible for 15 % of all culturally proven cases (Scholer 1980). This fungus has been reported many times in cutaneous (Baker *et al.* 1962, Gartenberg *et al.* 1978, Bottone *et al.* 1979, Yorifuji *et al.* 1989), gastrointestinal (Neame & Rayner 1960), osteomyelitis (Chaudhuri *et al.* 1992), or respiratory (Levy *et al.* 1986) forms. It was found to induce also mucormycosis developed by patients receiving hemodialysis (Kerr *et al.* 1988) and in lymphadenitis form of cattles and swine (Dion *et al.* 1987).

Rhizopus microsporus var. ***tuberosus*** R. Y. Zheng & G. Q. Chen, Mycotaxon 69: 183. 1998. – Fig. 12.

Colonies on PDA attaining 9 cm diam. in 3–4 days at 35 °C, low, only 1 mm high, dark gray to nearly black. Stolons well developed, light brown to brown, 10–25 μm diam., swollen and tuberose at places where rudimentary rhizoids are formed, but not swollen with normal rhizoids. Rhizoids absent or present, mostly very rudimentary, appearing as minute to conspicuous outgrowths from the tuberose part of the stolons, very rarely well-developed, simple, pale brown to brown, subhyaline at the distal end. Sporangiophores arising directly from aerial hyphae and not opposite rhizoids, simple or forked, or solitary, 2–4 (–5) in groups, simple, mostly arising from the tuberose part of the stolons, rarely from the non-swollen part and opposite rhizoids, brown to dark brown, paler at the upper part, 35–200 (–410) μm in length, 6.5–12 (–14.5) μm diam., mostly slightly widening upwards, sometimes equal throughout, smooth, straight to slightly curved, non-septate, occasionally with a swelling just beneath the apophysis. Apophyses evident. Sporangia globose to subglobose, 35–95 μm diam., blackish, quickly deliquescing, usually leaving no collar. Columellae variable, ovoid, ellipsoid, conical, 22–60 × 18.5–55 μm, subglobose, 18–42 μm diam., or applanate, 9–42 × 20–45 μm, straight or oblique, sometimes asymmetrical, pale brown or pale grayish brown, smooth

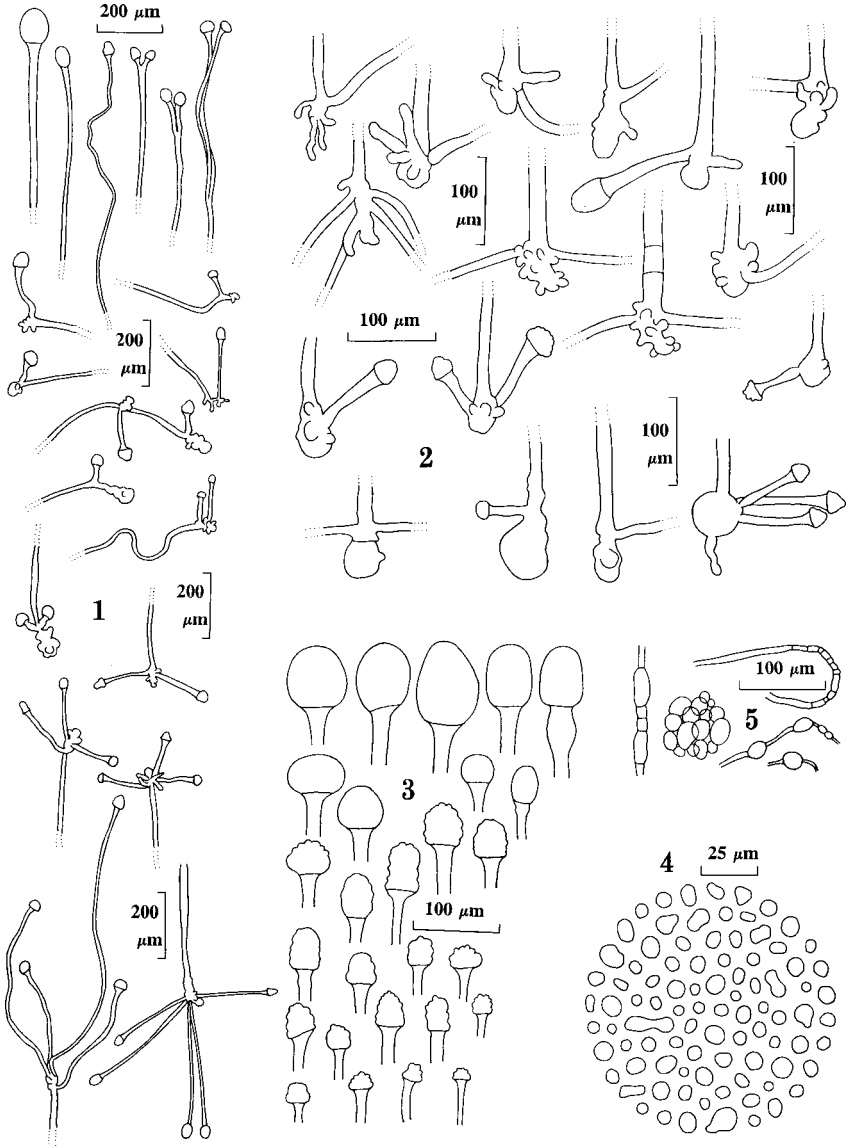

Fig. 12. *Rhizopus microsporus* var. *tuberosus*. 1. General characteristics of sporangiophores. Upper portion: sporangiophores which arise directly from aerial hyphae and without rhizoids, simple or forked. Lower portion: sporangiophores arising from stolons, with rudimentary to well developed rhizoids. 2. Enlarged basal parts of sporophores, showing various kinds of rhizoids which are rudimentary and arise as minute or conspicuous outgrowths from the tuberose part of the stolons, or well developed and arise from the normal region of the stolons. 3. Columellae of various shaped. Note that they are smooth in the larger ones and roughened in the smaller ones, usually without a collar. 4. Sporangiospores of various shapes. 5. Chlamydospores. [1–5. R-215 (=AS 3.1145), ex-Type].

in the larger ones and evidently roughened in the smaller ones. Sporangiospores heterogeneous in shape and size, mostly globose, subglobose to broadly ovoid, 4.5–8 μm diam., or 5.5–10 × 5–9 μm, others irregular in shape and larger, 10.5–20 × 6.5–9 μm, smooth to subsmooth, not striate, grayish when single, dark gray in mass. Chlamydospores solitary, in short chain, or in mass, yellow, 13.5–32 μm diam. Zygosporic state unknown, probably heterothallic.

Maximum growth temperature: 47 °C

DNA length of respectively entire ITS region (including 5.8S), *pyrG* gene intron 1 and intron 2: 606, 60, 50 bp.

Strain studied: R-215 (= AS 3.1145; from Chinese koji, Taishan County, Guangdong Prov., China; ex-Type of *R. microsporus* var. *tuberosus*).

Characterization of *R. microsporus* var. *tuberosus:* (1) rhizoids are mostly very rudimentary, appearing as minute to conspicuous outgrowths from the tuberose part of the stolons, very rarely developed normally like other taxa; (2) sporangiophores are generally single, simple, or forked at the apical part and arising directly from the aerial hyphae not opposite rhizoids, sometimes solitary or 2–4 (–5) in groups, arising from the tuberose part of the stolon, very rarely from the non-swollen stolons opposite normal rhizoids, generally widening upwards, sometimes equal in width throughout, not septate, occasionally with a swelling just beneath the apophysis; (3) sporangia are 35–95 μm in diameter, usually leaving no collar after deliquescing; (4) columellae are variable in shape, larger ones smooth, smaller ones roughened; (5) sporangiospores are heterogenous in shape and size, not striate; (6) zygosporic state is unknown.

The variety has been found only once (Zheng & Chen 1998). The unique morphology of the tuberose parts on the stolons is very stable and remained unchanged for more than 50 years.

Rhizopus niveus M. Yamaz., J. Soc. Agr. Tokyo 202: 586. 1919. – Fig. 13.

Colonies on PDA reaching 9 cm diam. in 3–5 days at 30 °C, floccose, about 1 cm high, somewhat depressed at the central part, white, slightly yellowish when aged. Hyphae 4.5–18.5 μm diam., aerial mycelia typically twisted tightly into hyphal knots here and there, sparsely septate. Stolons well developed, not septate or rarely septate. Rhizoids usually simple and finger-like, rarely branched, obtuse or somewhat pointed at the tip. Sporangiophores arising from stolons, mostly with opposite rhizoids, solitary, sometimes 2–3 in groups, a few arising from hyphae and

indeterminate, straight, substraight to curved, simple, rarely forked at the upper part, 70–529 μm long, equal to subequal in width throughout, 5–11.5 (–15) μm diam., often light yellowish brown to deep yellow, a few colourless, not septate, occasionally with a swelling, smooth. Apophyses conspicuous. Sporangia globose or slightly depressed globose, 41–82.5 (–106) μm diam., at first grayish, then brownish gray, nearly black when mature, breaking or slow deliquescing, quite often deliquescing after detaching as a whole from the columella, collar absent or small to conspicuous. Columellae globose to subglobose and 25–66 μm diam., broadly ovoid to ellipsoid and 27.5–69 × 23–64 μm, or hemispherical to roundish conical and 23–51 × 27.5–60 μm, granulous, light yellowish brown or light grayish brown. Sporangiospores subovoid or oblong-ovoid, 5–9 (–12.5) × 3.5–7 (–8) μm, roundish and 4–7 (–8) μm diam., subsmooth to subangulate, striation very faint to nearly invisible, subhyaline when solitary, dark gray in mass. Chlamydospores solitary, in short chain or in mass, hyaline or yellow, 9–36.5 × 7–23 μm. Zygosporic state not found, probably heterothallic.

Maximum growth temperature: 40–41 °C

DNA length of respectively entire ITS region (including 5.8S), *pyrG* gene intron 1 and intron 2: 538-540, 56, 58 bp.

Strain studied: **IFO 4759** (= AS 3.4816; from Chinese koji, China; received as, and ex-Type of *R. niveus*), IFO 4810 (= AS 3.4817; from Chinese koji, China; received as *R. niveus*).

Characterization of *Rhizopus niveus:* (1) colonies are consistently white and only slightly yellowish when aged; (2) aerial mycelia are typically twisted tightly into hyphal knots; (3) sporangiophores are mostly arising from stolons opposite rhizoids; (4) rhizoids are usually finger-like and seldom branched; (5) striation of sporangiospores are very faint and nearly invisible; (6) zygosporic state is not yet reported.

This species has been found only twice in China and was reported by M. Yamazaki in 1919. We have been trying very hard to reisolate this fungus from all kinds of samples collected in many districts of China but failed.

Rhizopus niveus is morphologically pertaining to the *R. microsporus* Group but molecularly it is inseparable from *R. arrhizus* & allies. For example, the entire ITS and 5.8S rDNA length for both *R. niveus* and *R. arrhizus* is 535-541 bp; the introns 1 & 2 of *pyrG* gene are respectively 56 bp and 58 bp in both these species (Liu *et al.* 2007). Besides, the maximum growth temperature of the two strains of *R. niveus* also falls within the maximum growth temperature

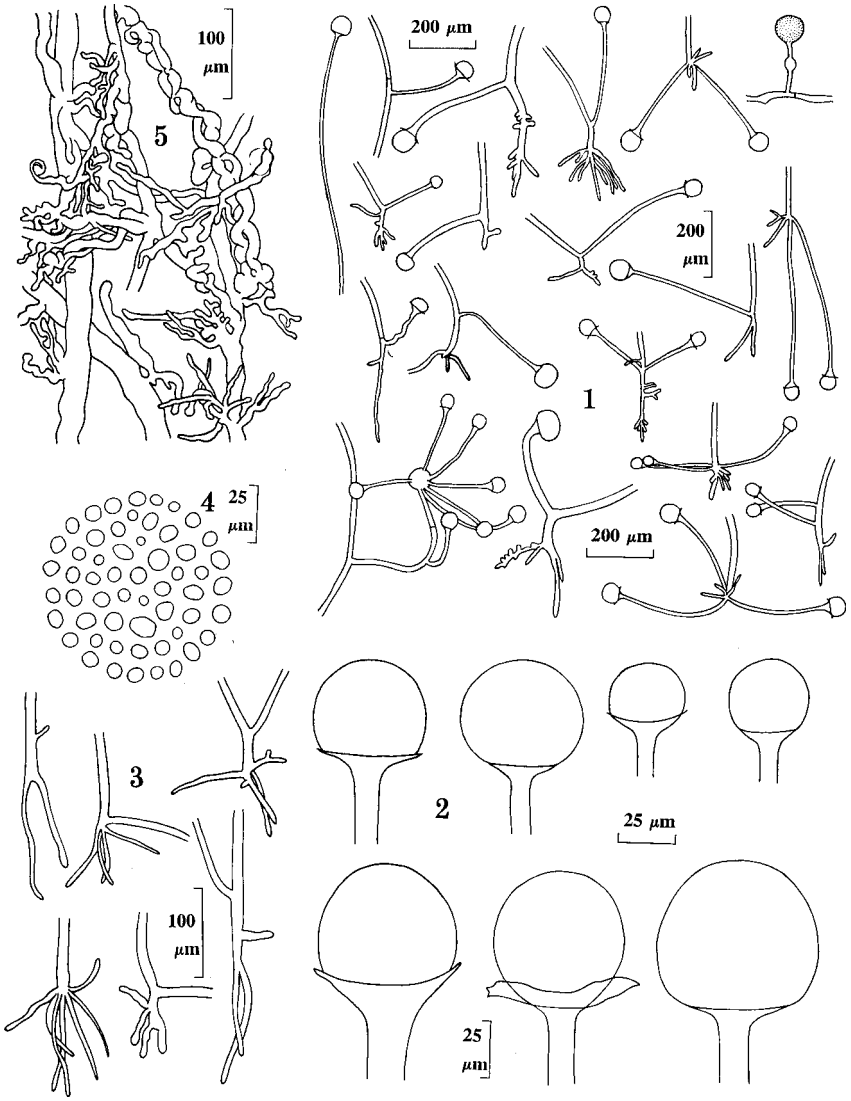

Fig. 13. *Rhizopus niveus:* 1. General characteristics of sporangiophores. Note that they are mostly arising from stolons with opposite rhizoids, equal to subequal in width throughout, occasionally with a swelling. 2. Columellae of various shapes, with or without a collar. 3. Rhizoids which are finger-like and rarely branched. 4. Sporangiospores with striation very faint to nearly invisible. 5. Aerial mycelia which are typically twisted tightly into hyphal knots. [1–5. IFO 4759 (= AS 3.4816), ex-Type].

range of *R. arrhizus* (40–42 °C). Nevertheless, in our classification, morphology always takes precedence over all the other criteria, and thus *R. niveus* is still retained as an independent species here.

Rhizopus reflexus Bainier, Bull. Soc. Bot. France 1880: 226. 1880. – Figs. 14 a & 14 b.

= *Rhizopus reflexoides* Phillipov, Bol. Rast. No. 4: 178. 1926.

= *Rhizopus stolonifer* (Ehrenb.: Fr.) Vuill. var. *lyococcos* (Ehrenb.) Stalpers & Schipper *in* Stalpers, Stud. Mycol. 24: 68. 1984.

= *Rhizopus stolonifer* var. *reflexus* (Bainier) Schipper, List of Cultures. Centraalbureau voor Schimelcultures, The Netherlands. p. 294. 1994. (nom. inval., Art. 33.2)

= *Rhizopus circinans* sensu auct.: Zycha *in* Rabenhorst, Kryptogamenflora der Mark Brandenburg VIa: 110. 1935; Kocková-Kratochvilová & Palkoska, Preslia 30: 159. 1958; Zycha, Siepmann & Linnemann, Mucorales. p. 74. 1969; non Tiegh., Ann. Sci. Nat., Ser. 6, 4: 369. 1876.

Colonies on PDA attaining 9 cm in 3–4 days at 20 °C, 5–12 mm high, often white at the central portion and black at the periphery; reverse dirty white. Stolons well developed, hyaline, brown, to dark brown, smooth. Rhizoids well developed, short to reaching 2000 μm long, repeatedly branching several times, more often branching at the terminal portion, grayish brown to dark brown, usually not septate. Sporangiophores typically nodding at the apex in at least some of them, usually arising from stolons opposite rhizoids, solitary or 2–5 (–7) in groups, simple, rarely divided at the upper portion when arising from mycelia and not opposite rhizoids, (190–) 400–1410 (–2400) μm long, (9–) 11.5–27 (–32) μm diam., equal in width throughout, sometimes widening at the bending part, smooth to slightly roughened, mostly straight, substraight, to slightly undulating, deep to dark brown, paler upwards, not septate. Apophyses evident. Sporangia globose to somewhat depressed-globose, (71–) 94–215 (–284) μm diam., blackish brown, deliquescing quickly in water, leaving no collar. Columellae ovoid, oblong-ovoid to oblong-cylindric and (53–) 71–177 (–205) × (49–) 59–141 (–196) μm, hemi-spherical or roundish conical and (23.5–) 53–127 (–153) × (41–) 82–165 (–196) μm, globose to subglobose and 82–118 (–141) μm diam., light grayish brown to light yellowish brown, deeper at the upper portion. Sporangiospores ovoid, subglobose to somewhat irregular, (4–) 5.5–10 (–14) × (3.5–) 5–7.5 (–10) μm, very rarely reaching 30 μm long, or (3.5–) 5–10 (–14.5) μm diam., indistinctly to distinctly angulate, distinctly striate. Giant cells absent. Chlamydospores absent. Zygosporangia globose to somewhat irregularly globose, slightly compressed or not compressed between the suspensors, 106–153 μm diam., blackish brown when mature, with blunt wart-like projections. Zygospores subglobose and 59–106 μm diam., or broadly ovoid and 94–146 × 82–135 μm, with dense and

obtusely pointed projections, hyaline, wall medium in thickness. Suspensors equal in shape and size, gradually widening upwards and constricted at the base, 59–94 μm diam. and 59–177 (–212) μm long, often heavily incrusted, light brown, non-septate, rarely 1 (–2) septate. Heterothallic.

Maximum growth temperature: (31–) 32–33 °C

DNA length of respectively entire ITS region (including 5.8S), *pyrG* gene intron 1 and intron 2: 656–658, 46, 56 bp.

Strains studied: CBS 319.35 (= AS 3.4998 = ATCC 44468; +, substrate and locality unknown; received as *R. stolonifer* var. *lyococcus*), CBS 320.35 (= AS 3.4999 = ATCC 44469; –, substrate and locality unknown; received as *R. stolonifer* var. *lyococcus*), **JCM 5589** (= AS 3.5074; -, from rotten leaves of *Arum maculatum*, Paris, France; received as *'R. circinans'*, ex-Type of *R. reflexus*), R-11 (= AS 3.824; +, substrate unknown, Japan; received as *R. reflexus*), R-12 (= AS 3.3459; +, from rotten fruit, Taian, Shandong Prov., China), R-583 (= AS 3.5616; from air, Beijing, China).

Characterization of *Rhizopus reflexus:* (1) colonies are generally white at the central portion and black at the periphery; (2) rhizoids develop very well, and are short to as long as 2000 μm; (3) sporangiophores are typically nodding at the apex in at least some of them; (4) collars are usually absent; (5) sporangiospores are quite variable in size; (6) both giant cells and chlamydospores are absent; (7) zygosporangia and zygospores usually form when opposite sex of mating partners are being brought together; (8) the two suspensors supporting a zygosporangium are equal in shape and size, and often heavily incrusted; (9) zygospores are covered with dense and obtusely pointed projections all over the surface; (10) sexual reproduction is heterothallic.

The correct name for this fungus is *R. reflexus* Bainier published in 1880. Despite *R. circinans* Tieghem (1876) is a much smaller fungus, Zycha (1935) mistakenly thought that *R. circinans* and *R. reflexus* were conspecific and substituted the earlier name *R. circinans* for *R. reflexus*. Kocková-Kratochvilová & Palkoska (1958) followed this scheme. Stalpers (1984) and Schipper (1984) recognized this fungus at varietal rank, using *'lyococcos'* as varietal epithet as they believed *Sporotrichum lyococcos* Ehrenb. (1818) and *R. reflexus* were the same. Many years later, in the CBS List of Cultures, 33rd edition 1994 (Anonymous 1994), the name was changed to *R. stolonifer* var. *reflexus* (Bainier) Schipper, which was a nomen invalidum in light of the Art. 33.2 of ICBN (Greuter *et al.* 2000).

In this study, we accept all the four taxa, i.e. *R. americanus* (= *R. sexualis* var. *americanus*), *R. reflexus* (= *R. stolonifer* var. *lyococcos*), *R. sexualis*, and *R. stolonifer* in the *R. stolonifer* Group at the rank of species. Our results of the sequence analyses of the entire ITS

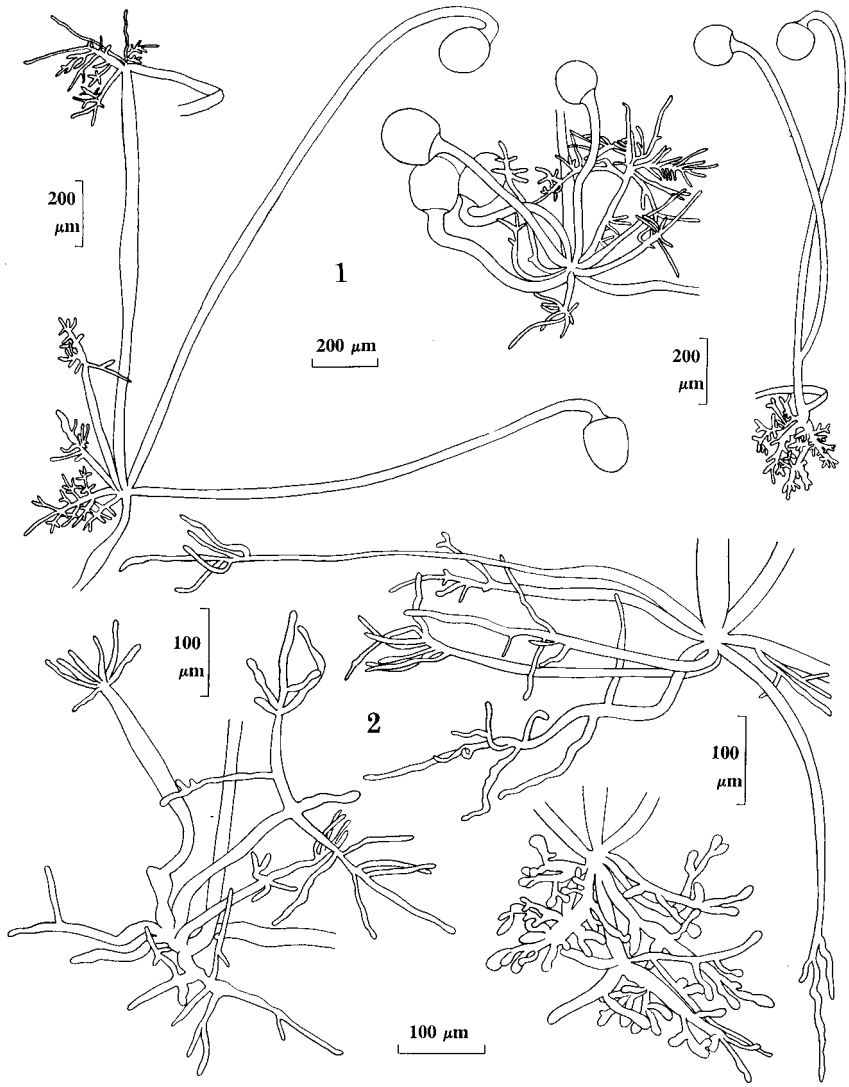

Fig. 14a. *Rhizopus reflexus:* 1. General characteristics of sporangiophores. Note that some of the sporangia are nodding and some are not. 2. Rhizoids of various lengths. [1–2. JCM 5589, ex-Type].

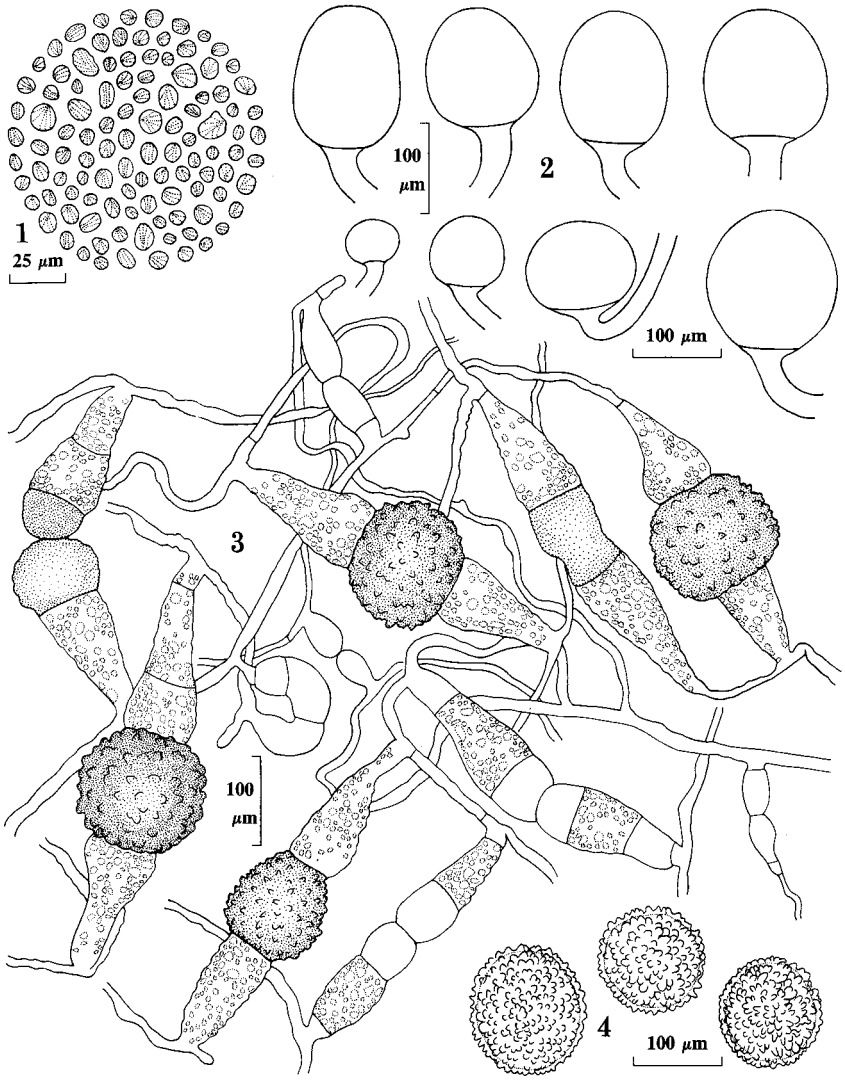

Fig. 14b. *Rhizopus reflexus:* 1. Sporangiospores. 2. Columellae. 3. Zygosporogenesis. Note that the two suspensors are equal in shape and size, and heavily incrusted. 4. Zygospores. [1–2. JCM 5589 (= AS 3.5074), ex-Type; 3, 4. R-11 (=AS 3.824) (+) × CBS 320.35 (–)].

rDNA and the partial *pyrG* support this treatment (Liu *et al*. 2007). Abe *et al*. (2006) on the one hand, indicated that *R. stolonifer* var. *stolonifer* and *R. stolonifer* var. *lyococcos* (*R. reflexus*) could be reclassified into two distinct species, because the latter did not cluster with the former and were located in a distinct position in all the three phylogenetic trees based on rDNA 18S, ITS, and 28S D1/D2 sequences; on the other hand, they pointed out that, owing to the formation of the sexual state between these two varieties reported by Schipper (1984), there are strong reasons too, for maintaining the two varieties as belonging to the same species. In our own studies, crosses between *R. stolonifer* and *R. reflexus* usually resulted in the formation of zygosporangia but no "true zygospores" were formed. It is not clear whether the "zygospores" formed between var. *stolonifer* and var. *lyococcos* are zygosporangia or zygospores in the work of Schipper (1984). Even they are true zygospores, in our experience, the formation of zygosporangia or zygospores is quite easy to encounter between two strongly compatible strains of different species in the Mucorales and should not affect their classification if morphology is distinctive enough and especially supported by molecular evidences.

Rhizopus schipperae Weitzman, McGough, Rinaldi & Della-Latta, Mycotaxon 59: 220. 1996. – Fig. 15.

Colonies on Czapek's agar very thin and transparent, almost invisible, covering the entire surface of the Petri dish in 4–5 days at 27–28 °C with good sporulation; on PDA thick and compact, also attaining 9 cm diam. in 4–5 days at 27–28 °C, white, becoming vinaceous-tawny after one week due to the formation of fructifications in the central portion. Stolons well developed, hyaline, with 2-several septa and often swollen to 25 μm diam. at the place where rhizoids are formed. Rhizoids simple or branched, 0 (–2) septate, short and stout to long and slender, usually stiff, brownish at the upper part, becoming colourless towards the tip, 15–340 μm long. Sporangiophores typically arising from stolons and opposite rhizoids, rarely from stolons without opposite rhizoids, solitary or 2–4 (–10) in groups, straight to substraight, seldom bending, mostly simple, sometimes in pairs and arising from a common bulbous base, 153–282 (–341) μm long, equal in width throughout, 5–9 μm diam., sometimes tapering upwards and 4.5–7.5 μm diam. at the uppermost portion, light grayish brown, paler upwards, colourless at the tip, often with 1 (–2) basal septa, rarely in the central portion, smooth. Apophyses not evident. Sporangia globose or subglobose, 23.5–53 (–70) μm diam., brownish black, deliquescing, usually without collar. Columellae quite regular in shape, mostly roundish conical and 13.5–30 × 18.5–34.5 μm or broadly ovoid and 20.5–37 × 18.5–35 μm, rarely subglobose and 15–32 μm diam., light grayish brown,

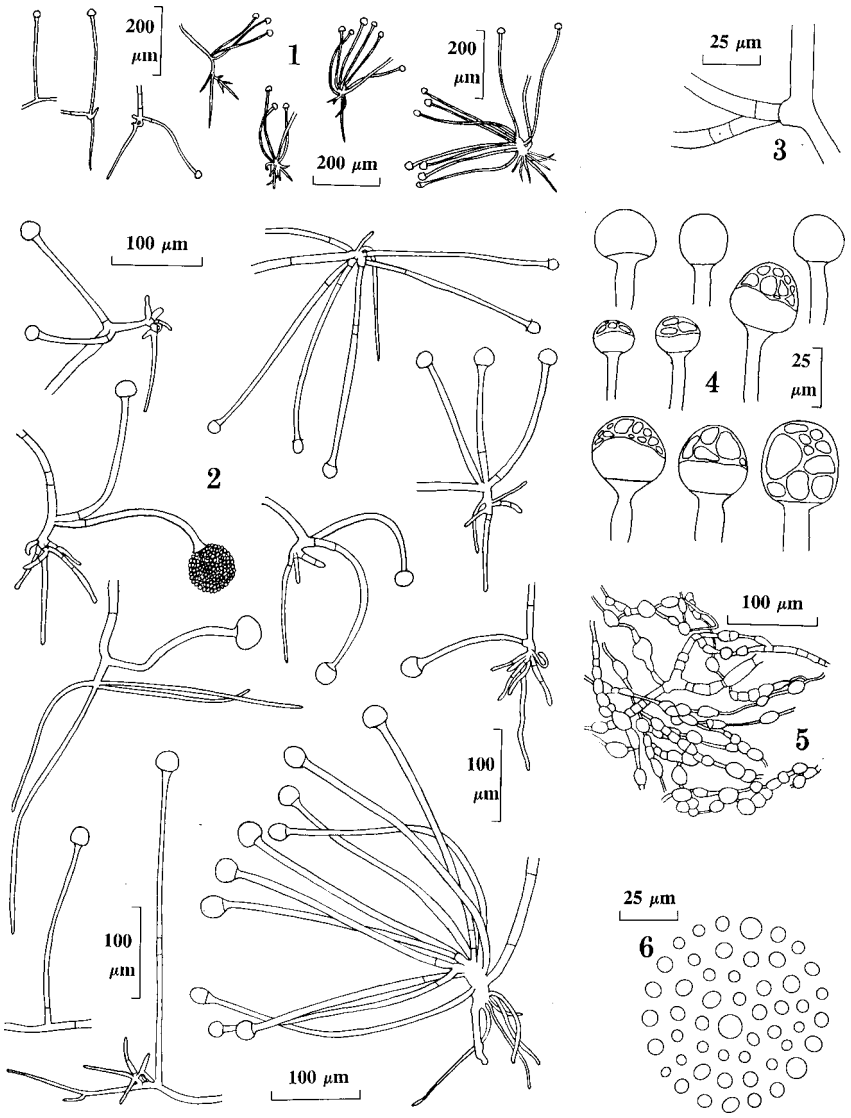

Fig. 15. *Rhizopus schipperae:* 1. General characteristics of sporangiophores. 2. Same, with higher magnification to show the details. 3. Basal parts of a pair of sporangiophores arising from a common bulbous base. 4. Columellae. Most of them are with pigment sedimentation at the upperhalf part. 5. Chlamydospores. 6. Sporangiospores. [1-6. ATCC 96514 (= AS 3.5767), ex-Type].

often deep brown in the upperhalf which seems to be sedimented with pigments. Sporangiospores rather regular in shape and size, broadly ovoid and 4–7 (–8) × 3.5–6.5 µm or subglobose and 4.5–7 (–8) µm diam., smooth to subsmooth, striation faint, hyaline when single, brown in mass. Chlamydospores solitary, in mass, or in short chains, yellow in colour, 13.5–51 × 9–28 µm diam. Zygosporic state unknown, probably heterothallic.

Maximum growth temperature: 45 °C

DNA length of respectively entire ITS region (including 5.8S), *pyrG* gene intron 1 and intron 2: 450, 66, 63 bp.

Strain studied: **ATCC 96514** (= AS 3.5767; from human lung, San Antonio, Texas, USA; received as, and ex-Type of *Rhizopus schipperae*).

Characterization of *Rhizopus schipperae:* (1) colonies on Czapek's agar are very thin and transparent, but with good sporulation, while on PDA thick, white, then vinaceous due to the formation of fructifications at the central portion; (2) stolons often strikingly inflate at the place where rhizoids are formed; (3) rhizoids are typically stiff and slender; (4) sporangiophores usually arise from stolons opposite rhizoids, solitary or 2–4 (–10) in groups, sometimes in pairs and from a common bulbous base; (5) sporangiophores often possess 1 (–2) basal septa; (6) collars are usually absent; (7) the upperhalves of columellae are often sedimented with brown pigments; (8) sporangiospores are smooth to subsmooth and not angulate, with nearly invisible striation; (9) zygosporic state is not yet found.

R. schipperae is the smallest fungus among the *Rhizopus* taxa accepted by us. When grown on the Czapek's agar, only a thin layer of mycelium is formed, but when this is examined directly with a stereomicroscope, all structures can be clearly seen in details. Weitzman *et al.* (1996) have reported that sporangia were not formed on PDA, while we observed numerous sporangia at the upper portion of the colony center after one week on this medium.

Abe *et al.* (2006) suggested that *R. schipperae* should be treated as a species independent from any group since the relationship of this species to the *microsporus* group was not strong enough according to their results from rDNA 18S, ITS, and 28S D1/D2 sequencing. Actually, this is the only case in one of the phylogenetic trees, in the ITS tree, and not so in the other two trees.

Rhizopus sexualis (G. Sm.) Callen, Ann. Bot., N. S. 4: 791. 1940. – Figs. 16 a & 16 b.

≡ *Mucor sexualis* G. Sm., Trans. Br. Mycol. Soc. 22: 252. 1939. (Basionym)

= *Mucor artocarpi* Berk. & Broome, J. Linn. Soc. 14: 137. 1873.

= *Rhizopus artocarpi* (Berk. & Broome) Boedijn, Sydowia 12: 328. 1958. (nom. illeg., Art. 53.1); non *Rhizopus artocarpi* Racib., 1900.

Colonies on PDA and L-PDA attaining 9 cm in 4 days at 20 °C, 4–7 mm high, lower at the middle part, at first white, then dark gray; reverse dirty white. Stolons well developed, hyaline, 7–16 µm diam., smooth. Rhizoids usually present, simple and finger-like or branching many times, hyaline to light brown, sometimes septate. Sporangiophores arising directly from aerial mycelia and not opposite rhizoids, or more often arising from stolons opposite rhizoids, solitary or 2–8 in groups, simple, sometimes dichotomously branching 1–2 times, very rarely 3–5 verticillate, (260–) 1200–2100 (–2770) µm long, (10–) 18.5–32 (–41) µm diam., equal in width throughout, smooth, straight to subcurved, rarely and vigorously recurved, brown, generally nonseptate, very rarely with a septum. Apophyses moderately evident. Sporangia globose to somewhat depressed-globose, 59–177 (–200) µm diam., rapidly deliquescent in water and leaving no collar. Columellae ovoid or ellipsoid-ovoid and 59–129 (–177) × 49–106 (–139) µm, subglobose and 82–141 µm diam., roundish conical to applanate, 14–117 (–153) × 31–141 (–177) µm, sometimes not symmetrical and askew, grayish brown, with a bluish tint. *Sporangiospores* ovoid to irregular, 7–21 (–35) × 5.5–11 (–15.5) µm, or subglobose and 6–13.5 µm diam., indistinctly angulate, distinctly striate. Giant cells in substrate mycelia or from zygophores, quite abundant, irregular in shape, 35–164 × 23–106 µm, intercalary or acrogenous, hyaline to light dirty brown, with granular contents. Chlamydospores absent. Zygosporangia subglobose, often compressed between the suspensors, 64–164 µm diam., black when mature, with blunt wart-like projections. Zygospores mostly subglobose to broadly ovoid, 58–155 µm diam., with radiate and flattened ornament, ridges absent, typically pale brown, wall thin and easily broken. Suspensors usually equal in shape and size, always inflated, ovoid, constricted at the base, 47–94 µm diam., heavily incrusted, brownish, sometimes orange-brown, septa generally absent. Azygosporangia abundant, especially on oat meal agar, formed on substrate mycelia, 71–177 µm diam. Homothallic.

Maximum growth temperature: 26–27 °C

DNA length of respectively entire ITS region (including 5.8S), *pyrG* gene intron 1 and intron 2: 734, 63, 0 bp.

Strains studied: **CBS 336.39** (= AS 3.4822 = CBS 340.62 = NRRL 2567; from rotten strawberry, Cambridge, England; received as, and ex-Type of *R. sexualis* var. *sexualis*), **CBS 340.62** (= AS 3.4822 = CBS 336.39 = NRRL 2567), **NRRL 2567** (= AS 3.4822 = CBS 336.39 = CBS 340.62).

Characterization of *Rhizopus sexualis:* (1) colonies are lower at the middle part; (2) rhizoids are mostly present and dichotomously branching 1-several times at the apex; (3) sporangiophores are simple, 1 (–2) times dichotomously branching, or rarely 3–5 verticillate;

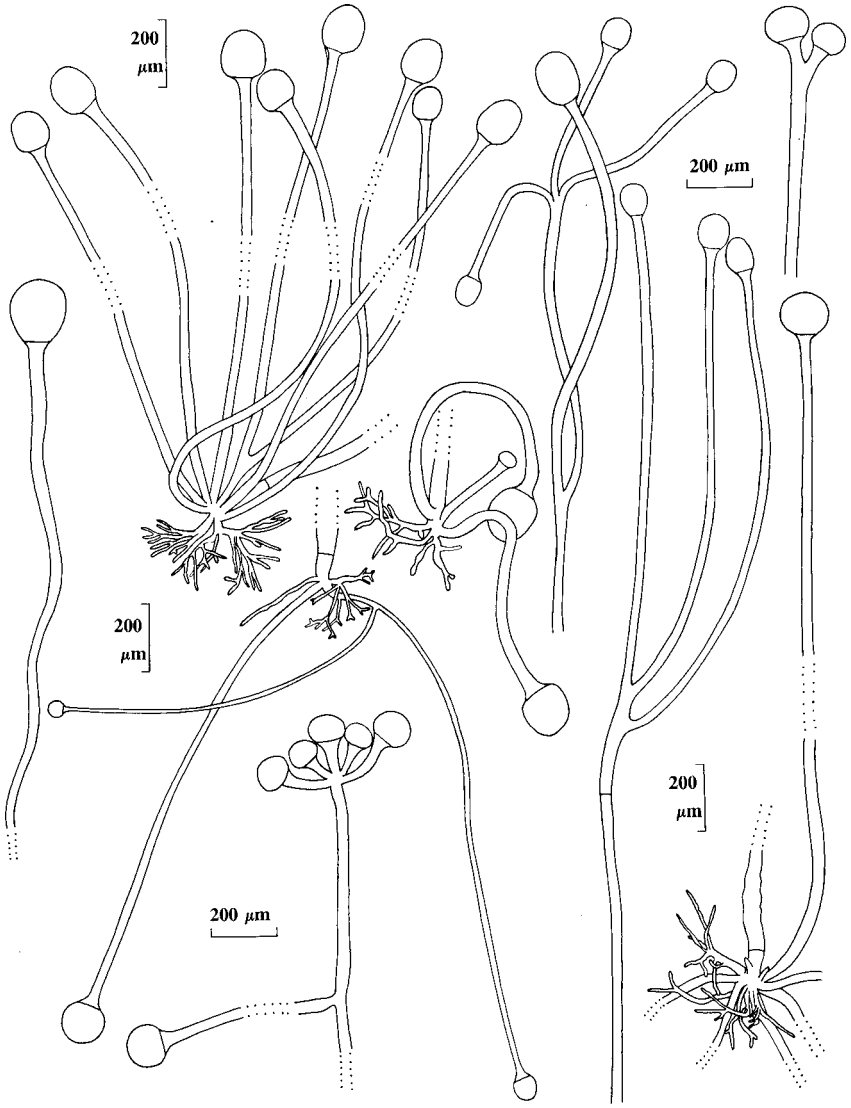

Fig. 16a. *Rhizopus sexualis:* General characteristics of sporangiophores. Note that they are either arising directly from aerial mycelia and without rhizoids or from stolons opposite rhizoids; also that they are simple, 1(–2) times dichotomously branched or rarely verticillate. [NRRL 2567 (= AS 3.4822), ex-Type].

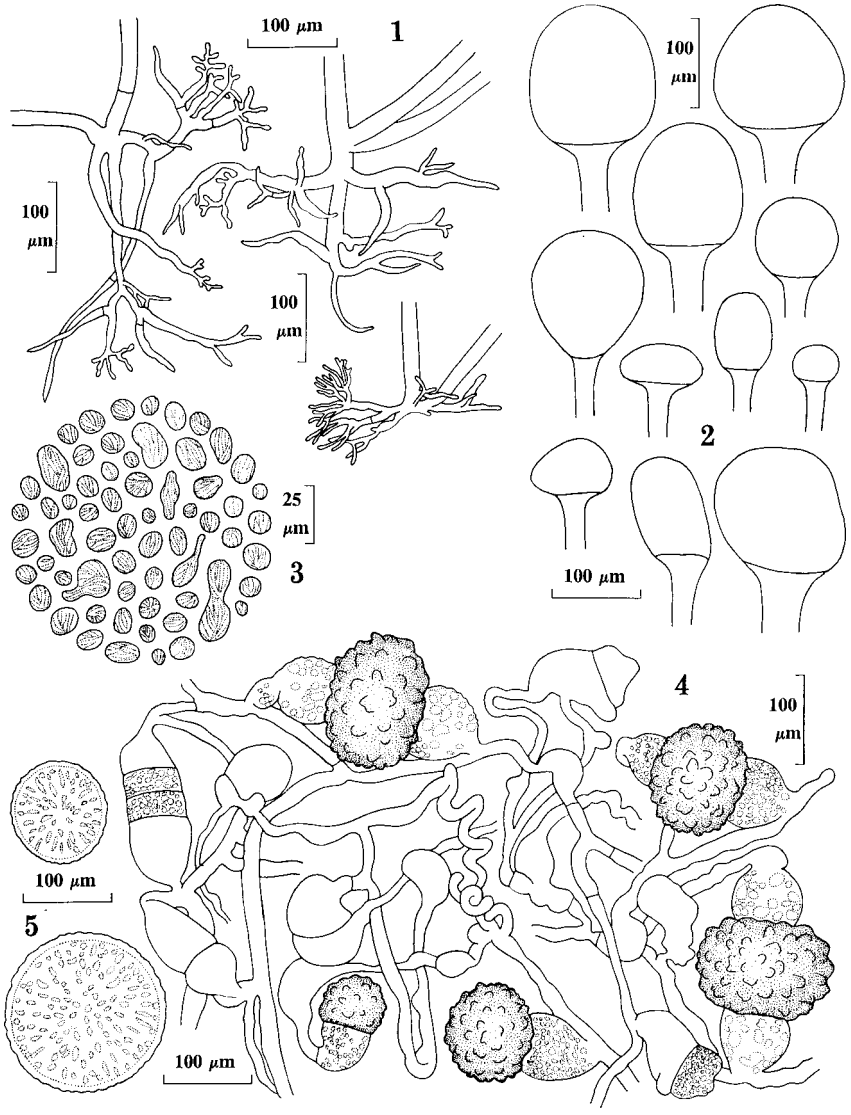

Fig. 16b. *Rhizopus sexualis:* 1. Rhizoids which are dichotomously branching 1-several times at the tips. 2. Columellae of various shapes. 3. Sporangiospores of various shapes and sizes. 4. Zygosporogenesis and azygosporogenesis. 5. Zygospores with radiate and flattened ornamentations. [NRRL 2567 (= AS 3.4822), ex-Type].

(4) sporangiophores are substraight, curved to vigorously recurved and usually equal to subequal in width throughout; (5) sporangia after deliquesced in water usually leave no collar behind; (6) giant cells are abundant on substrate mycelia or zygophores; (7) zygospores are thin-walled, with radiate and flattened ornamentations but without ridges, and typically pale brown in colour; (8) the two suspensors supporting a zygosporangium are usually equal in shape and size, always inflated and constricted at the base, also heavily incrusted and without septa; (9) azygosporangia are especially abundant on oat meal agar; (10) sexual reproduction is homothallic.

One of the difficult problems to solve in the classification of *Rhizopus* is the relationship among *R. stolonifer, R. sexualis, R. artocarpi* Racib., and *R. artocarpi* (Berk. & Broome) Boedijn. What we can definitely conclude is: *R. stolonifer* and *R. sexualis* are two different fungi since the type cultures of both are available for study, and the original diagnoses as well as the descriptions provided by other authors are clear enough to distinguish them. The most striking difference being that: in *R. stolonifer,* the sexual behavior is heterothallic, the two suspensors supporting a zygosporangium are typically enlarging gradually toward the zygosporangium with a long conical shape; while in *R. sexualis*, the sexual behavior is homothallic, and the two suspensors supporting a zygosporangium are typically enlarging abruptly into a globose shape.

Regarding *R. artocarpi* Racib. and *R. artocarpi* (Berk. & Broome) Boedijn, the relationship between themselves and the relationships of each of these two names to *R. stolonifer* or *R. sexualis* are very obscure. No type material of either name is available for study. However, when diagnoses of these two taxa are carefully read and compared, we have reasons to believe that *R. artocarpi* Racib. is more likely to be heterothallic than homothallic, and, on the contrary, *R. artocarpi* (Berk. & Broome) Boedijn is more likely to be homothallic than heterothallic. According to Raciborski (1900), zygospores of *R. artocarpi* Racib. were found on one of his agar cultures and not on living hosts. In the diagnosis, the suspensors of *R. artocarpi* Racib. were described as equal in size, 90–120 μm long, conical, enlarging towards the zygospore and up to 70 μm wide. The 2:1 ratio of length:width of the suspensors, and the equality in size of the two suspensors supporting a zygosporangium, as well as the greater possibility of being heterothallic, are all suggesting that *R. artocarpi* Rac. is conspecific with *R. stolonifer.* On the contrary, according to Boedijn (1958), zygospores of *R. artocarpi* (Berk. & Broome) Boedijn were numerous on the living male inflorences of the host, and were described as having suspensors of equal size enlarging abruptly into a gobose form; together with the greater possibi-

lity of being homothallic, it is most possibly conspecific with *R. sexualis*. As a result, we treat *R. artocarpi* Racib. as a synonym of *R. stolonifer*. The latter is a sanctioned name and takes precedence over the earlier published name *R. artocarpi* Racib. (See Art. 15.1 of ICBN). At the same time, *R. artocarpi* (Berk. & Broome) Boedijn is treated as a synonym of *R. sexualis*.

Milko *et al.* (1966), Pidoplichko & Milko (1971), and Milko (1974), despite the fact that *R. artocarpi* (Berk. & Broome) Boedijn is a later homonym of *R. artocarpi* Racib., still maintained this name as correct and treated *R. sexualis, R. artocarpi* Racib. as its synonyms.

Abe *et al.* (2006) reported that both varieties of *R. sexualis*, var. *sexualis* and var. *americanus* (*R. americanus*) had multiple distinct ITS sequences in a single strain. However, in our studies both taxa had only one distinct ITS sequence in either one test (*R. sexualis*) or after two repeated tests (*R. americanus*) (Liu *et al.* 2007).

Rhizopus stolonifer (Ehrenb. : Fr.) Vuill., Rev. Mycol. 24: 54. 1902. – Figs. 17a & 17 b.

≡ *Mucor stolonifer* Ehrenb., Silvae Mycol. Berol. p. 25. 1818 : Fr., Syst. Mycol. 3: 321. 1829. (Basionym)

= *Rhizopus nigricans* Ehrenb., Nova Acta Acad. Leop. 10: 198. 1820.

= *Ascophora mucedo* (L.) Tode, Fungi Mecklenb. Sel. 1: 13. 1790 : Fr., Syst. Mycol. 3: 310. 1832. p.p. (nom. rej.)

= *Rhizopus nigricans* var. *luxurians* J. Schröt., Krypt. Flor. Schles. Pilze. p. 207. 1886.

= *Rhizopus necans* Massee, Roy. Gard., Kew, Bull. Miscel. Inform. Nos. 122-123: 89. 1897.

= *Rhizopus artocarpi* Racib., Parasit. Algen Pilze Javas 1: 11. 1900.

Colonies on PDA attaining 9 cm in 3–4 days at 20 °C, reaching 10 mm high, often white at the central portion and black at the periphery; reverse dirty white. Stolons well developed, hyaline, smooth. Rhizoids vigorous, usually repeatedly branching many times and reaching 1000 μm long, hyaline to brown, sometimes septate. Sporangiophores usually arising from stolons opposite rhizoids, solitary or 2–5 (–9) in groups, simple, rarely forked at the upper portion, (400–) 850–2700 (–4000) μm long, (8–) 12–35 (–49) μm diam., equal in width throughout, sometimes slightly widening upwards, smooth to slightly roughened, straight, subcurved or rarely undulating, dark brown, becoming paler upwards, grayish brown at the apical part, often nonseptate. Apophyses evident. Sporangia globose to somewhat depressed globose, (47–) 82–224 (–274) μm diam., blackish brown, mostly deliquescing very quickly in water, leaving no collar. Columellae ovoid or oblong-ovoid and (53–) 82–177 (–212) × (47–) 76–153 (–182) μm, roundish conical, (18–) 35–118 (–165) × (33–) 47–141 (–177) μm, globose to subglobose, (29–) 59–141 (–196) μm, light grayish-brown or light yellowish brown, deeper at

the upper portion. Sporangiospores ovoid, subglobose, sometimes irregular, (4.5–) 5.5–12.5 (–19) × (4–) 5–9 (–14) µm or (4–) 5–11 (–16) µm diam., indistinctly or distinctly angulate, distinctly striate. Giant cells absent. Chlamydospores absent. Zygosporangia subglobose, often compressed between the suspensors, (94–) 106–153 (–200) µm diam., dark brown to blackish brown when mature, with blunt wart-like projections. Zygospores subgloobose and (65–) 92–130 (–153) µm diam. to broadly ovoid, 94–141 × 82–130 µm, with protuberances, hyaline, wall medium in thickness. Suspensors usually equal in shape and size, gradually widening upwards and constricted at the base, (45–) 56–100 (–113) µm diam. and (94–) 112–206 (–255) µm long, slightly incrusted to not incrusted, light brown, nonseptate, rarely 1 (–2)-septate. Heterothallic.

Maximum growth temperature: 30–32 °C

DNA length of respectively entire ITS region (including 5.8S), *pyrG* gene intron 1 and intron 2: 788, 82, 0 bp.

Strains studied: CBS 107.76 (= AS 3.4996; -, from decaying root of *Amorphophallus*, Indonesia; received as *Rhizopus stolonifer* var. *stolonifer*), CBS 108.76 (= AS 3.4997; +, substrate and locality unknown; received as *R. stolonifer* var. *stolonifer*), **CBS 150.83** (from *Artocarpus heterophyllus*, Malaysia; received as *R. stolonifer* var. *stolonifer*, ex-Type of *'R. artocarpi* Racib.'), **IFO 4781** (= AS 3.5051; –, substrate and locality unknown; received as *R. stolonifer* var. *stolonifer*, ex-Type of *R. nigricans*, Neotype of *R. stolonifer* newly designated in this study), IFO 5781 (= AS 3.5059; +, substrate and locality unknown; received as *'R. oryzae'*, originally as *R. nigricans*), IFO 30795 (= AS 3.5062; +, substrate and locality unknown; received as *'R. oryzae'*, originally as *R. stolonifer*), R-146 (= AS 3.5541; from fallen flower, Jinghong, Yunnan Prov., China), R-150 (= AS 3.5542; from sweet wrapping, Xishuangbanna, Yunnan Prov., China), R-153 (= AS 3.5544; from cow dung, Xishuangbanna, Yunnan Prov., China), R-154 (= AS 3.5545; from faded flower, Simao, Yunnan Prov., China), R-159 (= AS 3.5546; from soil under a bamboo, Chengdu, Sichuan Prov., China), R-160 (= AS 3.5547; from lawn soil, Chengdu, Sichuan Prov., China), R-163 (= AS 3.5548; from sweet wrapping, Guanxian, Sichuan Prov., China), R-164 (= AS 3.5549; from soil under a bamboo, Wolong, Sichuan Prov., China), R-168 (= AS 3.5550; from corncob left on the ground, Guiyang, Guizhou Prov., China), R-169 (= AS 3.5551; from sweet wrapping, Fanjingshan, Guizhou Prov., China), R-172 (= AS 3.5552; substrate and locality unknown, China), R-173 (= AS 3.5553; –, from faded flower, Dalian, Liaoning Prov., China), R-174 (= AS 3.5554; from fallen jasmine flower, Yantai, Shangdong Prov., China), R-175 (= AS 3.5555; from faded rose, Weihai, Shandong Prov., China), R-176 (= AS 3.5556; –, from faded chrysanthemum flower, Weihai, Shandong Prov., China), R-182 (= AS 3.5557; substrate and locality unknown), R-184 (= AS 3.5558; substrate unknown, Mentougou, Beijing, China), R-185 (= AS 3.5559; +, substrate unknown, Mentougou, Beijing, China), R-186 (= AS 3.5560; substrate unknown, Mentougou, Beijing, China), R-188 (= AS 3.5561; substrate unknown, Mentougou, Beijing, China), R-190 (= AS 3.5562; from hawthorn fruit, Beijing, China), R-193 (= AS 3.5563; substrate unknown, Mentougou, Beijing, China), R-194 (= AS 3.5564; substrate unknown, Mentougou, Beijing, China), R-201 (= AS 3.5565; +, from animal dung, Zhelimumeng, Nei Monggol Autonomous Region, China), R-202 (= AS 3.5566; from mulberry, Zhelimumeng, Nei Monggol Autonomous Region, China), R-203 (= AS 3.5567; from cow dung, Zhelimumeng, Nei Monggol Autonomous Region, China),

R-204 (= AS 3.5568; –, from sweet potato, Beijing, China), R-240 (= AS 3.5569; from fallen leaf, Zhongshan, Guangdong Prov., China), R-241 (= AS 3.5570; from soil under a shrub, Zhongshan, Guangdong Prov., China), R-250 (= AS 3.5571; from fallen flower, Xisha Islands, Hainan Prov., China), R-251 (= AS 3.5572; from fallen pepper, Xinglong, Hainan Prov., China), R-252 (= AS 3.5573; from rice, Diaoluoshan, Hainan Prov., China), R-253 (= AS 3.5574; from sugarcane, Diaoluoshan, Hainan Prov., China), R-254 (= AS 3.5575; from sugarcane, Diaoluoshan, Hainan Prov., China), R-255 (= AS 3.5576; from a kind of rice food wrapping, Jianfengling, Hainan Prov., China), R-256 (= AS 3.5577; from rice, Bawangling, Hainan Prov., China), R-257 (= AS 3.5578; from soil, Shaanxi Prov., China), R-258 (= AS 3.5579; from soil, Shaanxi Prov., China), R-259 (= AS 3.5580; from fallen flower, Xishuangbanna, Yunnan Prov., China), R-260 (= AS 3.5581; from cucumber flower, Simao, Yunnan Prov., China), R-261 (= AS 3.5582; from faded flower, Xishuangbanna, Yunnan Prov., China), R-262 (= AS 3.5583; from fallen fruit, Xishuangbanna, Yunnan Prov., China), R-551 (= AS 3.5584; from sweet wrapping, Guanxian, Sichuan Prov., China), R-552 (= AS 3.5585; from Panda dung, Wolong, Sichuan Prov., China), R-553 (= AS 3.5586; from rotten bamboo root, Wolong, Sichuan Prov., China), R-554 (= AS 3.5587; from false indigo flower, Shenyang, Liaoning Prov., China), R-555 (= AS 3.5588; from moldy mushroom, Harbin, Heilongjiang Prov., China), R-556 (= AS 3.5589; from sausage casing, Harbin, Heilongjiang Prov., China), R-557 (= AS 3.5590; from faded flower, Harbin, Heilongjiang Prov., China), R-558 (= AS 3.5591; from faded flower, Harbin, Heilongjiang Prov., China), R-559 (= AS 3.5592; from fallen fruit, Wuyishan, Fujian Prov., China), R-560 (= AS 3.5593; from paper on ground, Dinghushan, Guangdong Prov., China), R-561 (= AS 3.5594; from egg shell, Guangzhou, China), R-562 (= AS 3.5595; from cigarette case, Guangzhou, China), R-563 (= AS 3.5596; from sweet wrapping, Guangzhou, China), R-564 (= AS 3.5597; from sweet wrapping, Guangzhou, China), R-565 (= AS 3.5598; from fallen flower, Guangzhou, China), R-566 (= AS 3.5599; from rotten peach, Beijing, China), R-567 (= AS 3.5600; from animal dung, Miaofengshan, Beijing, China), R-568 (= AS 3.5601; from flower, Menyuanxian, Qinghai Prov., China), R-569 (= AS 3.5602; from chrysanthemum flower, Xining, Qinghai Prov., China), R-570 (= AS 3.5603; from bark of ginkgo, Beijing, China), R-571 (= AS 3.5604; from mung bean cake, Beijing, China), R-572 (= AS 3.5605; from soil in a zoo, Chengdu, Sichuan Prov., China), R-573 (= AS 3.5606; from soil, Guiyang, Guizhou Prov., China), R-574 (= AS 3.5607; from soil, Guiyang, Guizhou Prov., China), R-575 (= AS 3.5608; from grassland soil, Baotou, Nei Monggol Autonomous Region, China), R-576 (= AS 3.5609; from soil under a flower, Yinchuan, Ningxia Prov., China), R-577 (= AS 3.5610; from rotten strawberry, Beijing, China), R-578 (= AS 3.5611; from mouse dung, Zhangjiajie, Hunan Prov., China), R-579 (= AS 3.5612; from moldy seeds, Zhangjiajie, Hunan Prov., China), R-580 (= AS 3.5613; from sweet wrapping, Wanxian, Sichuan Prov., China), R-581 (= AS 3.5614; from cow dung, Hetian, Xinjiang Uygur Autonomous Region, China), R-582 (= AS 3.5615; from forest soil, Shansi, Guangxi Prov., China).

Characterization of *Rhizopus stolonifer:* (1) colonies are often white in the central portion and black at the periphery, reaching 10 mm high or more; (2) rhizoids grow vigorously, often repeatedly branch many times, may attain a length of 1000 μm, and are typically in bundles; (3) sporangiophores mostly arise from stolons opposite rhizoids and are solitary or 2–5 (–9) in groups and reaching 4000 μm in length; (4) sporangia deliquesce quickly in water and leave no collar; (5) sporangiospores are distinctly to indistinctly angulate and always distinctly striate; (6) zygosporangia are depress-

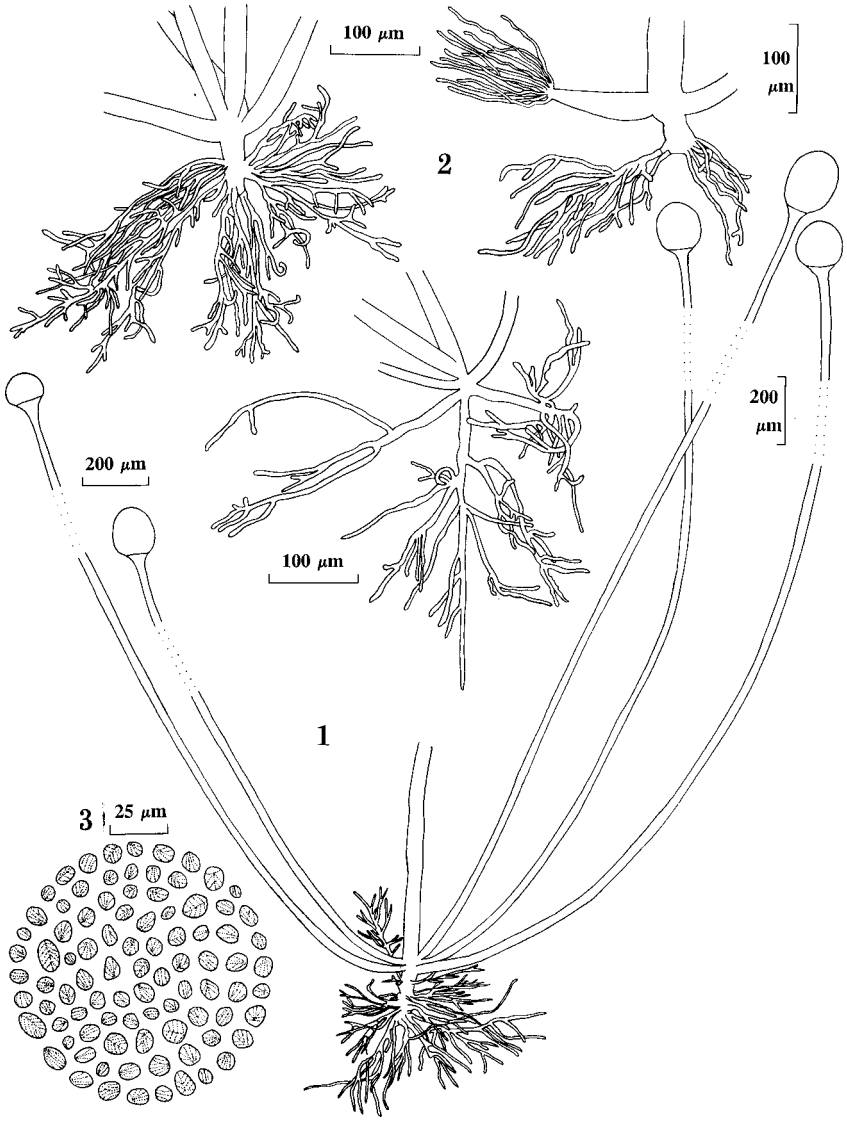

Fig. 17a. *Rhizopus stolonifer:* 1. General characteristics of a group of sporangiophores. Note that the sporangia are never nodding. 2. Rhizoids which are very well developed and repeatedly branching. 3. Sporangiospores. [1–3. IFO 4781 (= AS 3.5051), ex-Neotype].

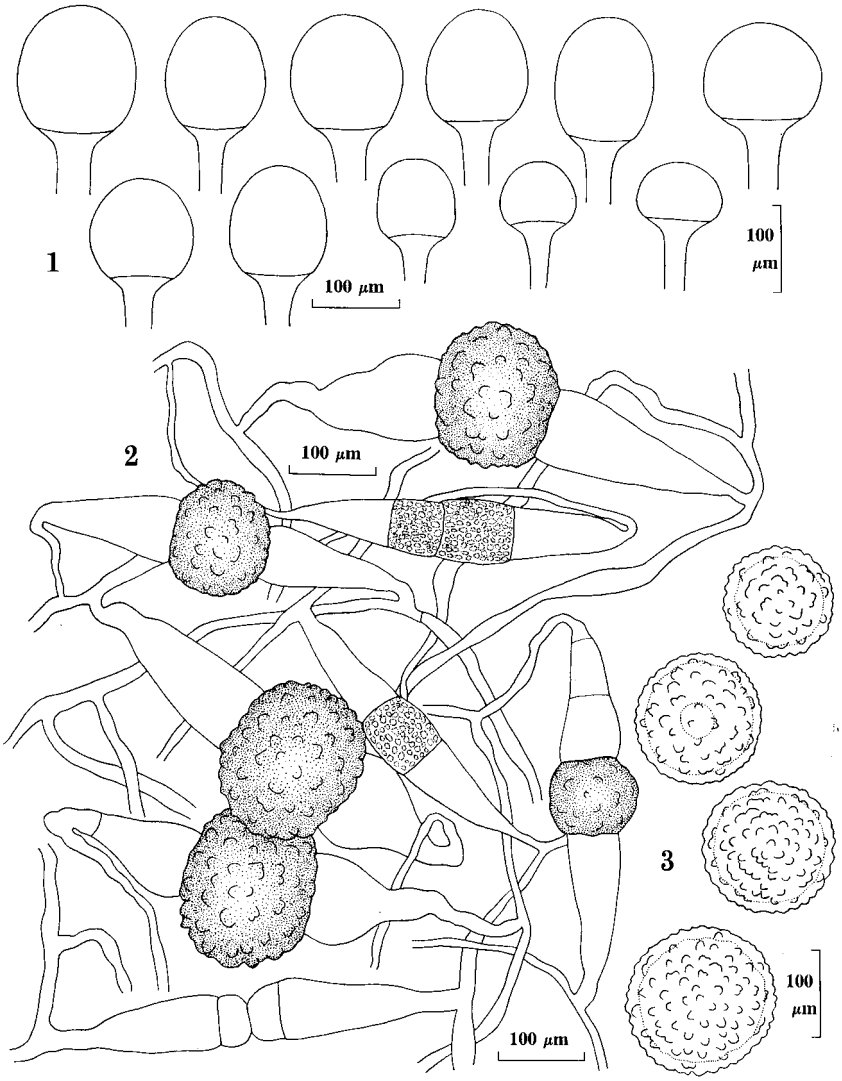

Fig. 17b. *Rhizopus stolonifer:* 1. Columellae of various shapes. 2. Zygosporogenesis. Note that the two suspensors are equal in shape and size, but not heavily incrusted. 3. Zygospores detached from zygosporangia. [1. IFO 4781 (= AS 3.5051), ex-Neotype; 2, 3. CBS 108.76 (= AS 3.4997) (+) × IFO 4781(–)].

ed-globose to subglobose; (7) zygospore wall is medium in thickness and verruculose; (8) the two suspensors which support a zygosporangium are generally equal in shape and size, and never heavily incrusted; (9) mating ability of this species is quite strong as compared to the other species in the same genus; (10) sexual reproduction is heterothallic.

One of the strains studied, CBS 150.83, was cited as the type culture of *R. artocarpi* Racib. when received. However, in the CBS List of Cultures, 33rd ed. 1994, CBS 150.83 was recorded as isolated from *Artocarpus heterophyllus* in Malaysia (Anonymous 1994), while in the diagnosis of *R. artocarpi* Racib. it was said to be isolated from *Artocarpus incisa* in Java. Hence, CBS 150.83 could not be the proper type culture.

For reasons to recognize *R. reflexus* as an independent species instead of a variety of *R. stolonifer,* please see the discussion under *R. reflexus*. For reasons to synonymize *R. artocarpi* Racib. with *R. stolonifer*, please see the discussion under *R. sexualis*.

Doubtful Taxa

Rhizopus angulisporus (Saito) Naumov, Opredelitel Mukorovykh (Mucorales). p. 72. Izd-vo AN SSSR. 1935.

≡ *R. japonicus* var. *angulisporus* Saito, Zentbl. Bakt. ParasiKde, Abt. 2, 17: 102. 1907. (Basionym)

The basionym of this name, *R. japonicus* var. *angulisporus* was described by Saito (1907) as "having sporangiophores 200–700 μm long and 12 μm wide, sporangia 44–80 μm in diameter, columellae 20–56 μm in diameter, and sporangiospores 12–18 × 8 μm, with striation" which is doubtless a micro-*Rhizopus*, not being conspecific with *Rhizopus delemar* as considered by Pidoplichko & Milko (1971) and Milko (1974). If striation is not formed on the spores, this variety may well be a synonym of *R. microsporus* var. *oligosporus*. No type material can be studied; we therefore have to treat it as a doubtful taxon.

Rhizopus apiculatus McAlpine, Fungus Diseases of Stone-fruit Trees in Australia and Their Treatment. p. 96. 1902.

No type culture is available for study. The distinguishing characteristic of this fungus is the pointed apex of the columellae which has never been reported in any other taxa of *Rhizopus*. In Fig. 63 of McAlpine's book, a somewhat pointed columella can be faintly seen inside the sporangium.

Rhizopus bankul Hanzawa, Mycol. Centralbl. 1:406. 1912.

Rhizopus bankul was listed as one of the synonyms of *R. oryzae* (= *R. arrhizus* var. *arrhizus*) by Pidoplichko & Milko (1971) and

Milko (1974). No type or other material and no diagnosis are available for our study.

Rhizopus betivorus Nevod., Nauch. Zap. VNIS 6: 314. 1928. provisional name. (nom. inval., Art. 34.1)

Type culture and diagnosis could not be found. It seems to be a member of the *R. arrhizus* group based on the short descriptive key of Naumov (1939, spelled *'betavorus'*). Pidoplichko & Milko (1971) and Milko (1974) synonymized this name with *R. oryzae* (= *R. arrhizus* var. *arrhizus*).

Rhizopus biourgei S. F. Fang, Ann. Soc. Sci. Bruxelles, Sér. II, Sci. Nat. Med. 57: 113. 1937.

In the diagnosis, *R. biourgei* was described by Fang (1937) as "having sporangiophores up to 6 mm long and 10–30 μm diam., sporangia 50–150 μm diam., columellae reaching 130 × 130 μm, spores 3.5–5.5 × 6–7 μm, chlamydospores numerous and growing well at 35–37 °C". The extraordinary length of the sporangiophores was possibly a measure of those arising from mycelia and not from those arising from stolons. If this was the case, then *R. biourgei* can be assigned to the *R. arrhizus* Group, though we do not know which variety should be assigned to. No type culture is available.

Rhizopus cambodja (Chrzaszcz) Vuill., Rev. Mycol. 24: 45. 1905.
≡ *Mucor cambodja* Chrzaszcz, Zentbl. Bakt. ParasiKde, Abt. 2, 7: 334. 1901. (Basionym)

Kocková-Kratochvilová & Palkoska (1958), Pidoplichko & Milko (1971), and Milko (1974) assigned this name to *R. arrhizus* (as *R. oryzae* by the latter two authors). To us, this is a smaller fungus belonging to the *R. microsporus* Group, though we do not know which species or variety should be assigned to. No type culture is available.

Rhizopus candidus M. Yamaz., J. Soc. Agric. Tokyo 193: 1002. 1918.

R. candidus is probably a member of the *R. arrhizus* Group based on the Japanese description provided by Yamazaki (1918). No type culture is available.

R. circinans Tiegh., Ann. Sci. Nat., Sér. 6, 4: 369. 1876.

This name has been used by Zycha (1935), Kocková-Kratochvilová & Palkoska (1958), and Zycha *et al.* (1969) to replace *R. reflexus* Bainier. However, the sporangiophores of *R. circinans* are only 120–180 μm in length and far less than that of *R. reflexus*. No type culture is available, and the fungus has not been recovered since its discovery.

Rhizopus echinatus Tieghem, Ann. Sci. Nat., Sér. 6, 4: 370. 1876.

The species was described as having echinulate sporangiospores, a character which has never been reported in any other *Rhizopus* species. Lendner (1908), Naumov (1939), Kocková-Kratochvilová & Palkoska (1958), Zycha (1935), Zycha *et al*. (1969), and Milko (1974) recognized this species. We prefer to treat it as a doubtful species until it is rediscovered and proved to have echinulate spores.

Rhizopus equinus var. ***annamensis*** N. Bernard, Bull. Soc. Mycol. France 30: 232. 1914.

In the present study, we agree with Kocková-Kratochvilová & Palkoska (1958) and Zycha *et al*. (1969) in considering *R. equinus* Costantin & Lucet published in 1903 as conspecific with *R. microsporus* var. *microsporus*. Two of the important reasons are: the sporangiophores of both fungi are tapering upwards, and their sporangiospores are evidently striate. These two important characters cannot be found in *R. equinus* var. *annamensis;* hence it is a taxon that cannot be assigned to *R. microsporus* var. *microsporus* or *R. equinus*, no matter how closely it is related to *R. equinus*. According to the diagnosis, *R. equinus* var. *annamensis* is also a member of the *R. microsporus* Group, but not assignable to any known species or varieties of the same Group. No type material is available.

Rhizopus fructicola (Corda) Berl. & De Toni *in* Sacc., Sylloge Fungorum 7: 214. 1888.

≡ *Ascophora fructicola* Corda, Icones Fungorum hucusque cognitorum, Prag. 2: 20. 1838. (Basionym)

The description provided by Saccardo (1888) is too meager to determine the taxonomic position of this fungus.

Rhizopus hallerianus Rivolta, 1884.

No reference material including the citation of literature for this name could be found.

Rhizopus helminthophthorus de Bary & Keferst, Zeitschr. Wiss. Zool. 1861.

No reference material concerning this name could be found.

Rhizopus homothallicus var. ***indicus*** B. S. Mehrotra, 1967.

No reference material concerning this name could be found.

Rhizopus humilis M. Yamaz., J. Soc. Agric. Tokyo 193: 984. 1918.

R. humilis was reduced to synonymy with *R. liquifaciens* and *R. oryzae* (both = *R. arrhizus* var. *arrhizus*) by Yamamoto (1930) and

Milko (1974), respectively. But basing on the Japanese diagnosis written by Yamazaki (1918), *R. humilis* is a smaller fungus pertaining to the *R. microsporus* Group.

Rhizopus intermedius Amadori, Atti Soc. Toscana Sc. Pisa, Mem. 5: 37. 1934.

The brief description found on p. 65 of vol. 5 of Sylloge Fungorum provided by P. A. Saccardo (1972) was the only reference we have obtained concerning this fungus. The size of the sporangia, 60 μm, was the only measurement provided by that description. Therefore, *R. intermedius* possibly belongs to the *R. microsporus* Group.

Rhizopus japonicus var. ***angulisporus*** Saito, Zentbl. Bakt. ParasiKde, Abt. 2, 18: 101. 1907.

≡ *Rhizopus angulisporus* (Saito) Naumov, Opredelitel Mukorovykh (Mucorales). p. 72. Izd-vo AN SSSR. 1935.

See discussion under *R. angulisporus* for the details.

Rhizopus lendneri Zurikoff, 1919.

Reference material of whatever kind could not be obtained concerning this name.

Rhizopus minimus Tieghem, Ann. Sci. Nat., Sér. 6, 1: 84. 1875.

Lendner (1908) and Naumov (1939) accepted this species. Kocková-Kratochvilová & Palkoska (1958), Zycha *et al.* (1969), Pidoplichko & Milko (1971), and Milko (1974) synonymized it with *R. microsporus*. Although the diagnosis of *R. minimus* is very meager and brief, it remains to be a different species of a still smaller size other than *R. microsporus*.

Rhizopus niger (Ciagl. & Hewelke) Gedoelst *in* Guéguen, Champ. Paras. d. Homme et des Anim., p. 33, 1902.

≡ *Mucor niger* Ciagl. & Hewelke, Zeitschr. F. Klin. Med. 22: 626. 1893. (Basionym)

Original reference of this name is not available. In the descriptions provided by Lendner (1908) and Saccardo (1912), no measurement of any part of the fungus could be found. The fungus thus described is assignable to whatever species in *Rhizopus*.

Rhizopus nigricans var. ***minor*** C. N. Jensen, Bull. Agric. Exp. Sta. Cornell 315: 447. 1912.

The English diagnosis showed this fungus to be a member of the *R. arrhizus* Group. No type or authentic cultures are available.

Rhizopus nigricans var. ***minutus*** Chaudhuri & Sachar, Sydowia 32: 91. 1934.

The variety is very similar to *R. nigricans* var. *minor* C. N. Jensen. Tandon (1968) synonymized both varieties, but using the earlier name *R. nigricans* var. *minor* as the synonym of the later name *R. nigricans* var. *minutus*. Milko (1974) reduced both varieties to synonymy with *R. nigricans* (= *R. stolonifer*). In our opinion, these two varieties are more likely to be a member of the *R. arrhizus* Group. We think it is better to treat them as doubtful rather than to merge them with a much larger fungus like *R. stolonifer*.

Rhizopus nigricans var. ***verticillatum*** Demelius, Verh. Zool.-Bot. Ges. Wien 64: 489. 1916.

Milko (1974) reduced this name to synonymy with *R. oryzae* (= *R. arrhizus* var. *arrhizus*). Neither type culture nor diagnosis of this variety is available for study to clarify its taxonomic position.

Rhizopus olivacellus (Speg.) Naumov, Opredelitel Mukorovykh (Mucorales). p. 72. Izd-vo AN SSSR. 1935.

≡ *Mucor olivacellus* Speg., Fung. Argent. Nov., p. 204. 1899. (Basionym)

Based on the descriptions of *Mucor olivacellus* and *Rhizopus olivacellus* respectively provided by Saccardo (1902) and Naumov (1939), the fungus is probably a member of the *R. arrhizus* Group.

Rhizopus pestis-bovinae Hallier, 1873.

No reference material could be found for this name.

Rhizopus sakuranei

No information could be found concerning the author, literature and publication year.

Rhizopus sakuranei var. ***instriatus***

Same as above.

Rhizopus salebrosus var. ***instriatus*** Y. Takeda, J. Agric. Chem. Soc. Japan 4: 275. 1928.

Rhizopus salebrosus var. *instriatus* was said to be closely related to *R. salebrosus* but differing in the absence of spore striation by Takeda (1928). After a careful comparison of the two descriptions written by Yamazaki (1918) for *R. salebrosus* and Takeda (1928) for *R. salebrosus* var. *instriatus*, we believe the two names refer to different fungi. *Rhizopus salebrosus* is conspecific with *R. arrhizus* var. *delemar*; while *R. salebrosus* var. *instriatus* is a fungus intermediate between *R. arrhizus* var. *delemar* and *R. microsporus* var. *oligosporus*. For this reason, we synonymize *R. salebrosus* with *R. arrhizus* var. *delemar*, and treat *R. salebrosus* var. *instriatus* as doubtful.

Rhizopus speciosus (Oudem.) Lendn., Les Mucorinées de la Suisse. p. 125. 1908.

≡ *Mucor speciosus* Oudem., Overdr. Ned. Kr. Arch., 3 série, II, 3:720. 1902. (Basionym)

Neither the description of *R. speciosus* nor that of *Mucor speciosus* can give us any idea about the taxonomic position of this species. Naumov (1939) seems to be the only author who accepted *R. speciosus*. Kocková-Kratochvilová & Palkoska (1958) and Zycha *et al.* (1969) reduced it to synonymy with *R. microsporus*. However, the sporangial diameter of this fungus was described as 90–140 μm which is much larger than that of *R. microsporus*.

Rhizopus subtilis Bonord., 1851.

Nothing is known about this name.

Rhizopus suinus N. Nielsen, Virch. Arch. Path. Anat. Physiol. Klin. Med. 273: 859. 1929.

Schipper (1984) synonymized *R. suinus* with *R. oryzae* (= *R. arrhizus* var. *arrhizus*) after studying an authentic culture of this fungus, CBS 295.31, although she has already noticed that judging from its protologue, *R. suinus* should be a micro-*Rhizopus*. CBS 295.31 was also studied by us and reidentified as *R. arrhizus* var. *delemar*. Probably CBS 295.31 was contaminated and is no longer the original authentic culture of *R. suinus* anymore.

Rhizopus suinus f. ***sterilis*** N. Nielsen, Virch. Arch. Path. Anat. Physiol. Klin. Med. 273: 862. 1929.

The main difference between *R. suinus* f. *sterilis* and *R. suinus* is the failure of forming sporangia in the former (Nielsen 1929). This character is reminiscent of *R. arrhizus* var. *rouxii* (= *R. arrhizus* var. *arrhizus* in our study). Since the taxonomic position of *R. suinus* could not be determined, both the species and its form are better to be treated as doubtful.

Rhizopus tanekoji Hanzawa, Mycol. Centralbl. 1:408. 1912.

Like *R. bankul* Hanzawa, *R. tanekoji* was listed as one of the synonyms of *R. oryzae* (= *R. arrhizus* var. *arrhizus*) by Milko (1974). No type or other material as well as a diagnosis are available for our study. Both of them are treated as doubtful here.

Rhizopus umbellatus A. L. Sm., J. Roy. Micros. Soc. 1901: 618. 1901.

The English description of this taxon by A. L. Smith (1901) and especially the figure of this fungus, are reminiscent of a species of *Absidia* rather than *Rhizopus*. Since no culture is available, no conclusion can be drawn.

Excluded Taxa

Rhizopus artocarpi Racib. var. ***luxurians*** J. Schröt.

A search in the literature reveals that J. Schröter had never published such a name. Perhaps this is an error for *R. nigricans* var. *luxurians* J. Schröt. published in 1886.

Rhizopus betavorus Nevod., Hauch. Zap. VNIS 6: 314. 1928. (provisional name). (nom. inval., Art. 34.1)

The correct spelling of the epithet of this name should be *"betivorus"* which is treated as one of the doubtful taxa in this study.

Rhizopus chinensis var. ***chungyuen*** Wai, Bull. Inst. Chem. Acad. Sinica, Taiwan 9: 75. 1964.

This is one of the synonyms of *Actinomucor elegans* (Eidam) C. R. Benj. & Hesselt. (Anonymous 2004).

Rhizopus chiuniang var. ***isofermentarius*** Y. Takeda

Takeda has never published the name. This is possibly an error for *R. chunguoensis* var. *isofermentarius* Y. Takeda, published in 1935.

Rhizopus elegans Eidam, Jahres-Ber. Schles. Ges. Vaterl. Cultur 61: 232. 1884.

Like *R. chinensis* var. *chunyuen* Wai, this name is also a synonym of *Actinomucor elegans* (Benjamin & Hesseltine 1957).

Rhizopus javensis (Boedijn) Milko, Nov. Sist. Niz. Rast. 1968: 80. 1968.

This fungus is better to be accepted as *Rhizopodopsis javensis* Boedijn (1958).

Rhizopus lutescens (Link) Naumov, Opredelitel Mukorovykh (Mucorales). p. 132. Izd-vo AN SSSR. 1935. (nom. inval., Art. 33.1)

This name was not included in the text of Naumov's book (Naumov 1935), but appeared on the alphabetic list in the last and fourth part of the book as *"lutescens* (Link, 1824) N. Naumov comb. nov.". The content in the brackets, (Link 1824), was probably a hint to the basionym *Mucor lutescens* Link published in 1824. Since Naumov (1935) did not describe *lutescens,* and the brief description of *M. lutescens* provided by Saccardo (1888) did not show the fungus to be a member of *Rhizopus,* the only thing we can do is to exclude it from the genus.

Rhizopus norvegicus Hagem, 1908.

Mucor norvegicus was published by Hagem in 1908. Two years later, he reduced this name to synonymy with *M. nodosus* (Namysl.) Hagem (Hagem 1910), the basionym of which is *Rhizopus nodosus* Namysl. The reason for transferring *R. nodosus* to *Mucor nodosus* is that, in the classification of Hagem (1908), *Rhizopus* was treated as a subsection of the genus *Mucor* and not as an independent genus. In fact, Hagem had never published the combination *Rhizopus norvegicus*, what he had published was *Mucor norvegicus*.

Rhizopus oryzae G. Winter, 1895.

According to Stafleu & Cowan (1988), G. Winter was a German mycologist who died in 1887. Thus, he could not publish *Rhizopus oryzae* in 1895. This is probably a mistake for *R. oryzae* Went & Prins. Geerl.

Rhizopus parasiticus (Lucet & Costantin) Lendn., Matér. Flore Cryptog. Suisse 3: 115. 1908.

≡ *Rhizomucor parasiticus* Lucet & Costantin, C. r. hebd. Séanc. Acad. Sci., Paris 129: 1033. 1899. (Basionym)

This name is now known to be a synonym of *Rhizomucor pusillus* (Lindt) Schipper (= *Rhizomucor parasiticus*) (Schipper 1978).

Rhizopus ramosus (Lindt) Zopf *in* Schenk, Handbuch der Botanik 4: 587. 1890.

≡ *Mucor ramosus* Lindt, Arch. f. Exp. Pathol. u. Pharm. 21: 275. 1886. (Basionym)

This name is now known to be a synonym of *Absidia ramosa* (Lindt) Lendn. (≡ *Mucor ramosus*) (Hesseltine, 1950).

Rhizopus ramosus Moreau, Bull. Soc. Bot. France 60: 220. 1913. (nom. inval., Art. 53.1); non (Lindt) Zopf *in* Schenk, 1890.

The French description of this fungus is too meager for recognition, and also that the name *Rhizopus ramosus* Moreau is a later homonym of *R. ramosus* (Lindt) Zopf.

Rhizopus stolonifer var. ***luxurians*** J. Schröt., 1886.

Schröter had never published such a combination. Probably this is an error for the name *Rhizopus nigricans* var. *luxurians* J. Schröt. published in 1886.

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