

On Mucoraceae s. str. and other families of the Mucorales

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Summary. — The Mucoraceae are redefined and contain mainly the genera *Mucor*, *Circinomucor* gen. nov., *Zygorhynchus*, *Micromucor* comb. nov., *Rhizomucor* and *Umbelopsis* char. emend.

Mucor s. str. contains taxa with black, verrucose, scaly or warty zygospores (or azygospores), unbranched or only slightly branched sporangiophores, spherical, pigmented sporangia with a clavate or obclavate columella, and elongate, ellipsoidal sporangiospores. Typical species are *M. mucedo*, *M. flavus*, *M. recurvus* and *M. hiemalis*.

Zygorhynchus is separated from *Mucor* by black zygospores with walls covered with conical, often furrowed protuberances, small sporangia with a spherical or oblate columella, and small, spherical or rod-shaped sporangiospores. Some isogamous or agamous species are transferred from *Mucor* to *Zygorhynchus*.

Circinomucor is introduced for *Mucor circinelloides*, *M. plumbeus*, *M. racemosus* and their relatives. The genus is characterized by cinnamon brown zygospores covered with starfish-like projections, racemously or sympodially branched sporangiophores, spherical sporangia with a clavate or ovate columella and small, spherical or broadly ellipsoidal sporangiospores.

Micromucor is based on *Mortierella* subg. *Micromucor* and is close to *Mucor*. The genus is characterized by velvety colonies, small, light sporangia with an often reduced columella and small, subspherical sporangiospores. Zygospores are unknown. Typical species are *M. ramanniana* and *M. isabellina*.

Some *Mortierella* species of the subgenus *Micromucor* with umbellate, 1- or many-spored sporangia are included in the genus *Umbelopsis*.

Other genera of the former Mucoraceae are classified in two new families Absidiaceae and Phycomycetaceae. The Mortierellaceae, the Thamnidiaceae and the Radiomycetaceae are briefly discussed. A key to the families of the Mucorales is given.

Introduction

In Mucorales the delimitation of families and genera is mainly based on the vegetative, anamorphous structures, the sporangia or conidia. The teleomorph known as zygospores usually is neglected and has not or only incidently been used in keys to families and genera (e. g. HESSELTINE & ELLIS, 1973; O'DONNELL, 1979; v. ARX, 1981). A reason may be, that most of the Mucorales are heterothallic and form zygospores only in mating experiments. Moreover in many species and even genera zygospores are not known or have been observed

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only incidentally. In a few cases, however, mating experiments are required for a proper identification of species.

Some homothallic, *Mucor*-like species with unequal suspensors (gametangia, zygothores) have been classified by VUILLEMIN (1903) in a separate genus *Zygorhynchus*, but the delimitation from *Mucor* remained doubtful. It is well known that some *Mucor* species with equal suspensors or with azygospores are much closer to *Zygorhynchus* species than to other species of *Mucor* (SCHIPPER & al., 1975). The delimitation of *Mucor* and *Mortierella* is also doubtful. *Mortierella* is the largest genus of the Mucorales and contains about 70 mainly soil borne species (DOMSCH & al., 1980). Some of them, however, are much closer to *Mucor* than to typical species of *Mortierella* (BENJAMIN, 1979).

In this paper an attempt is made to introduce the characteristics of the zygothores for the delimitation of more natural families and genera. The Mucoraceae sensu stricto, the largest family of the Mucorales, are the main subject, other families being only briefly discussed. The study is mainly based on literature data, only a rather small number of fresh isolates and some strains of the CBS collection have been examined.

A. Mucoraceae DUMORTIER, char. emend.

Heterothallic or homothallic, colonies rapidly expanding; suspensors (gametangia, zygothores) formed on aerial hyphae or sporangiothores, equal or unequal, often swollen, opposite to the zygote; zygothores naked, cinnamon, dark-brown or black, spherical or nearly so, thick walled, verrucose, warty, spiny or ridged; sporangiothores erect or recurved, simple or branched, usually without swellings; sporangia spherical, without apophyses, usually many-spored (*Umbelopsis*: 1-spored), hyaline or pigmented, with a deliquescent wall and an usually distinct columella; sporangiospores 1-celled, hyaline or slightly pigmented, mostly smooth, rarely punctulate or warty. Type genus: *Mucor* MICHELI (ex FR.)

Close to the Mucoraceae are some genera of the Thamnidaceae (e. g. *Thamnidium* LINK, *Cokeromyces* SHANOR and *Backusella* J. ELLIS & HESSELTINE). All these genera have zygothores similar to those of *Zygorhynchus*. The only distinguishing character is the presence of 1-spored sporangia or of sporangia without columella.

Excluded from the Mucoraceae are taxa characterized by zygothores with a smooth, furrowed, verrucose or scaly wall (e. g. *Rhizopus* EHRENB.) and taxa with smooth zygothores surrounded by a hyphal envelope (e. g. *Phycomyces* KUNZE, *Absidia* van TIEGHEM or *Circinella* van TIEGHEM). Taxa with obovate or obpyriform sporangia or with a subsporangial, usually funnel-shaped apophysis also are excluded.

Typical Mucoraceae also do not form stolons, but submerged rhizoids may be present.

Key to the genera

1. Sporangia up to 25 μm diam, 1- or many-spored; colonies velvety. 2
1. Sporangia larger, many-spored 3
2. Sporangia in umbels, 1- or many-spored, without columella 5. *Umbelopsis*
2. Sporangia not in umbels, many-spored, usually with a small columella 4. *Micromucor*
3. Thermophilic; zygospores black, warty; sporangiospores small, spherical or nearly so; rhizoids often present 7. *Rhizomucor*
3. Mesophilic or psychrophilic, rhizoids usually absent 4
4. Parasitic on other Mucorales, suspensors of the zygospores with finger-like outgrowths 8. *Parasitella*
4. Not mycoparasitic; suspensors without outgrowths 5
5. Zygospores cinnamon-brown, with starfish-like projections; sporangiophores sympodially or racemously branched, with several, usually small sporangia; sporangiospores small, spherical or ellipsoidal; usually heterothallic 3. *Circinomucor*
5. Zygospores brown to black, verrucose, warty or with conical protuberances; sporangiophores not or only slightly branched or when much branched, sporangia at least some larger than 80 μm 6
6. Sporangiospores striate, with hairlike, polar appendages; suspensors equal 6. *Gilbertella*
6. Sporangiospores not striate, without appendages 7
7. Zygospores verrucose or warty (not spiny); suspensors equal; sporangia with a clavate or obclavate columella, often large; sporangiospores usually ellipsoidal; mainly coprophilous 1. *Mucor*
7. Zygospores with conical, often spine-like protuberances; suspensors equal or unequal; sporangia with a spherical or slightly oblate columella; sporangiospores usually small, ellipsoidal, spherical or rod-shaped; often soil-borne or isolated from plant debris 2. *Zygorhynchus*

1. **Mucor MICHELI** (1729) ex FR. — Syst. Mycol. 3: 317 (1832).
Type species: *M. mucedo* MICHELI ex FR.

Synonyms see O'DONNELL (1979).

Colonies rapidly expanding, grey, ochraceous or brown, with rather thick, expanding hyphae, usually rather high (1–4 cm); suspensors formed on expanding hyphae (not on sporangiophores), equal or slightly unequal, opposite; zygospores naked, often rather

large, dark-brown or black, verrucose, warty or with irregular projections; sporangiophores erect or recurved, long or short, often reaching several levels, simple or branched mainly at the base, rather stiff; sporangia apical, spherical, with an incrustated and pigmented, often finely echinulate wall and a distinct, large, obovate, clavate or ellipsoidal columella; sporangiospores ellipsoidal, often rather large; heterothallic or homothallic.

Key to the species

1. Largest sporangia with 100 μm diam. or more 2
- 1*. Largest sporangia smaller than 100 μm diam. 15
2. Young sporangiophores recurved, sporangiospores often large .. 3
- 2*. Sporangiophores erect from the beginning 6
3. Sporangia up to 350 μm , sporangiospores 30–40 \times 12–20 μm ..
..... 8. *M. oblongiellipticus*
- 3*. Sporangia and sporangiospores smaller 4
4. Sporangia up to 250 μm , sporangiospores 10–17 \times 6–10 μm ...
..... 9. *M. oblongisporus*
- 4*. Sporangia smaller 5
5. Sporangiospores roundish in outline, tuberculate
..... 19. *M. tuberculisporus*
- 5*. Sporangiospores ellipsoidal or ovate 15. *M. recurvus*
6. Psychrophilic, growth and sporulation at 10° C; sporangia up
to 220 μm 7
- 6*. Mesophilic, occasionally thermotolerant 8
7. Sporangia light, columellae conical 14. *M. psychrophilus*
- 7*. Sporangia dark, columellae ellipsoidal-clavate ... 18. *M. strictus*
8. Sporangia up to 400 μm , sporangiospores 22–40 \times 14–20 μm ,
columellae conical 12. *M. plasmaticus*
- 8*. Sporangia and sporangiospores smaller 9
9. Sporangia 200–350 μm , columellae often attenuated at base .. 10
- 9*. Sporangia with up to 190 μm diam. 11
10. Sporangia dark, up to 350 μm , sporangiospores ellipsoidal
..... 11. *M. piriformis*
- 10*. Sporangia grey-brown, up to 250 μm , sporangiospores often
cylindrical 7. *M. mucedo*
11. Sporangiophores often with some branches 12
- 11*. Sporangiophores usually unbranched 14
12. Sporangiospores 4–8 \times 3–5 μm 16. *M. saturninus*
- 12*. Sporangiospores 7–13 \times 4–7 μm 13
13. Colonies up to 1 mm high 1. *M. aligarensis*
- 13*. Colonies more than 1 mm high 2. *M. flavus*
14. Sporangiospores 4–8 \times 3–5 μm 6. *M. mousanensis*
- 14*. Some sporangiospores larger 4. *M. inaequisporus*
15. Sporangiospores longer than 10 μm 16

- 15*. Sporangiospores shorter than 10 μm18
 16. Columellae conical, sporangiospores 12—22 \times 9—13 μm
 20. *M. zychae*
 16*. Columellae obovate or ellipsoidal17
 17. Sporangiospores 10—20 \times 5—11 μm 10. *M. odoratus*
 17*. Sporangiospores 10—13 \times 4—6 μm 13. *M. prayagensis*
 18. Sporangia yellow, sporangiospores ellipsoidal-fusiform, 6—10 \times
 2—4 μm 5. *M. luteus*
 18*. Sporangia brown, sporangiospores ellipsoidal-cylindrical19
 19. Sporangiospores 3—5 \times 2—3.5 μm 17. *M. silvaticus*
 19*. Sporangiospores 5—9 \times 3—5 μm 3. *M. hiemalis*

List of species

1. *Mucor aligarensis* B. S. MEHROTA & B. R. MEHROTRA. — Sydowia 23: 183 (1969).
2. *Mucor flavus* BAINIER. — Bull. Soc. mycol. Fr. 19: 157 (1903).
3. *Mucor hiemalis* WEHMER. — Anns Mycol. 1: 37 (1903). — *Mucor corticolus* HAGEM [Anns Mycol. 8: 265 (1910)] can hardly be distinguished. — *Mucor genevensis* LENDNER [Mat. F. Crypt. Suisse, 3 (1908)] is a homothallic relative.
4. *Mucor inaequisporus* DADE. — Trans. Br. mycol. Soc. 21: 25 (1937). *Mucor variosporus* SCHIPPER [Stud. Mycol. 17: 11 (1978)]-can hardly be distinguished and is known by a single strain.
5. *Mucor luteus* LINNEMANN. — Flora 130: 195 (1936).
6. *Mucor mousanensis* BAIJAL & B. S. MEHROTRA. — Sydowia 19: 205 (1965).
7. *Mucor mucedo* L. — Spec. Plant. 2: 1655; ex Fr. — Syst. mycol. 3: 320. (1832).
8. *Mucor oblongiellipticus* NAGANISHI & al. ex PIDOPLICHKO & MILKO. — Atlas mucoral'nykh gribov, Kiev, p. 81 (1971).
9. *Mucor oblongisporus* NAUMOV. — Mater. Mikol. Fitopat. Ross. 1: 11 (1915).
10. *Mucor odoratus* TRESCHOW. — Bot. Tidskr. 45: 148 (1941).
11. *Mucor piriformis* FISCHER in Rabenh. Krypt. fl. 4: 191 (1892).
12. *Mucor plasmaticus* van TIEGHEM. — Anns Sci. nat. 1: 33 (1875).
13. *Mucor prayagensis* B. S. MEHROTRA & NAND ex SCHIPPER. — Stud. Mycol. 17: 16 (1978).
14. *Mucor psychrophilus* MILKO. — Atlas mucoral'nykh gribov, Kiev p. 73 (1971).
15. *Mucor recurvus* BUTLER. — Mycologia 44: 561 (1952).
16. *Mucor saturninus* HAGEM. — Anns Mycol. 8: 265 (1910).
17. *Mucor silvaticus* HAGEM. — Unters. Norweg. Mucorinee 1: 31 (1908). — SCHIPPER (1973) treated this species as a forma of *M. hiemalis*.
18. *Mucor strictus* HAGEM. — l. c. p. 18 (1908).

19. *Mucor tuberculisporus* SCHIPPER. — Stud. Mycol. 17: 23 (1978).
20. *Mucor zychnae* BAIJAL & B. S. MEHROTRA. — Sydowia 19: 204 (1965).

The above-mentioned species have been revised by SCHIPPER (1973; 1975; 1978). Her study was based exclusively on cultures maintained in the CBS culture collection. Some other species have been enumerated by ZYCHA & SIEPMANN (1969).

SCHIPPER (1973) reduced some of the species accepted here to formae of *M. hiemalis*. This was questioned by DOMSCH & al. (1980). The respective taxa are rather easy to distinguish by morphological characters, e. g. by the shape and size of the sporangia and sporangiospores. SCHIPPER based her conclusions on mating experiments, which, however, cannot be conclusive, because the zygospores have not been germinated.

ZYCHA & SIEPMANN (l. c.) and SCHIPPER (l. c.) enumerated some more species. Some of which may be identical to species mentioned above, others are doubtful or have to be excluded. A peculiar species is *Mucor azygosporus* R. K. BENJAMIN [Aliso 5: 240 (1963)] with azygospores on erect stalks, orange colonies, round columellae and broadly ellipsoidal, yellow, 7—11 × 6—8 µm sporangiospores.

2. *Zygorhynchus* VUILL. — Bull. Soc. mycol. Fr. 19: 116 (1903).

Type species: *Z. heterogamus* (VUILL.) VUILL. [= *Mucor heterogamus* VUILL.]

Colonies expanding, usually grey or blackish, low or rather high, with erect, only occasionally branched sporangiophores or zygophores; suspensors usually unequal, often borne laterally on sporangiophores, often on erect hyphae or zygophores, opposite; zygospores small (up to 90 µm), black, with conical, often furrowed protuberances; sporangia acropetal, spherical, rather small, with a deliquescent wall and a spherical or more often broader than high columella; sporangiospores spherical, subspherical, cubical, ellipsoidal or rod-shaped, small, often containing globules; usually homothallic, rarely heterothallic, mostly soil-borne or isolated from food or animals.

Key to the species

1. Sporangiospores spherical or nearly so 2
- 1*. Sporangiospores ellipsoidal or rod-shaped 5
2. Sporangia up to 60 µm, sporangiospores 2—4 µm 3
- 2*. Sporangia up to 90 µm, sporangiospores 4—7 µm 4
3. Zygospores black, up to 100 µm 5. *Z. heterogamus*
- 3*. Zygospores brown, up to 50 µm 3. *Z. californiensis*
4. Suspensors unequal, homothallic, heterogamous . . 4. *Z. exponens*

4*	Suspensors equal or nearly so, heterothallic, isogamous	1. <i>Z. amphibiorum</i>
5.	Sporangia up to 60 μm , sporangiospores usually rod-shaped . . . 6	
5*	Sporangia up to 80 μm , sporangiospores ellipsoidal 8	
6.	Suspensors equal or nearly so (isogamous).. 2. <i>Z. bacilliformis</i>	
6*	Suspensors unequal (heterogamous) 7	
7.	Mesophilic, no sporulation at 12° C 7. <i>Z. japonicus</i>	
7*	Psychrophilic, sporulation at 12° C, sporangiospores small	9. <i>Z. psychrophilus</i>
8.	Sporangiospores 2—3.5 μm broad, mesophilic, homothallic	8. <i>Z. moelleri</i>
8*	Sporangiospores 4—5 μm broad, thermotolerant, heterothallic	6. <i>Z. indicus</i>

List of species

1. *Zygorhynchus amphibiorum* (SCHIPPER) v. ARX, comb. nov.
= *Mucor amphibiorum* SCHIPPER. — Stud. Mycol. 17: 14 (1978).
The species is close to *Z. exponens*, probably identical. The suspensors may be equal or unequal.
2. *Zygorhynchus bacilliformis* (HESSELTINE) v. ARX, comb. nov.
= *Mucor bacilliformis* HESSELTINE. — Mycologia 46: 360 (1954).
3. *Zygorhynchus californiensis* HESSELTINE & al. — Mycologia 51: 185 (1959).
4. *Zygorhynchus exponens* BURGEFF. — Bot. Abhandl. 4: 34 (1924); HESSELTINE & al. — Mycologia 51: 185 (1959).
5. *Zygorhynchus heterogamus* (VUILL.) VUILL. — Bull. Soc. mycol. Fr. 19: 117 (1903).
6. *Zygorhynchus indicus* (LENDNER) v. ARX, comb. nov.
= *Mucor indicus* LENDNER. — Bull. Soc. bot. Genève 21: 258 (1930).
= *M. rouxianus* WEHMER (non *Amylomyces rouxii* CALMETTE).
This fungus has been isolated from food and decaying plants in warmer areas.
7. *Zygorhynchus japonicus* KOMINAMI. — Mykol. Zentralbl. 5: 1 (1915).
8. *Zygorhynchus moelleri* VUILL. — Bull. Soc. mycol. Fr. 19: 117 (1903).
This species has been described under several other names, enumerated by ZYCHA & SIEPMANN (1969). *Mucor subtilissimus* OUDEM. sensu SCHIPPER (1978) may represent an anamorphous state of this fungus, which in culture often forms only the sporangial state.
9. *Zygorhynchus psychrophilus* SCHIPPER & HINTIKKA. — Antonie van Leeuwenhoek 35: 29 (1969).

The classical species of the genus have been treated in detail by HESSELTINE & al. (1959).

3. *Circinomucor* v. ARX, gen. nov.

Mucor MICHELI sect. *Racemosus* ZYCHA. — Mucorineae, p. 16 (1935).

Mucor MICHELI sect. *Sphaerosporus* ZYCHA. — l. c.

Type species: *C. circinelloides* (van TIEGHEM) v. ARX.

Coloniae celeriter crescunt, ex hyphis latius, aeriis et rhizoidea immersae compositae; suspensores aequales, oppositi, in hyphis aeriis oriundi; zygosporae globosae, cinnamomeae, cristis et spinis stellaribus ornatae; sporangiophora sympodiala vel racemosa ramosa; sporangia globosa, usque ad 100 μm longa, columellis clavatis vel obovatis; spores parvae, globosae vel ellipsoideae; chlamydosporae saepe praesentes; genus heterothallicum.

Species typica: *Mucor circinelloides* van TIEGHEM.

Colonies light, expanding, composed of rather broad aerial hyphae and rhizoids; suspensors (zygophores) borne on aerial hyphae, usually equal, opposite; zygosporae subspherical, cinnamon-brown or copper coloured, ornamented by often starfish-like arranged ridges and spines, rather small; sporangiophores sympodially or racemously branched; sporangia spherical, up to 100 μm , with a clavate, obpyriform or ellipsoidal columella; sporangiospores small, spherical or broadly ellipsoidal, up to 10 μm diam; intercalary chlamydosporae often present; usually heterothallic.

Diagnostic characters of the genus are the cinnamon-brown zygosporae with starfish-like projections and the repeatedly branched sporangiophores. The genus is closer to *Zygorhynchus* and *Parasitella* than to *Mucor*. The zygosporae are similar to those of *Cunninghamella*.

Key to the species

1. Columellae with apical wart-like projections, sporangiospores subspherical, punctulate 6. *C. plumbeus*
- 1*. Columellae without apical projections 2
2. Sporangiospores (sub-)spherical 3
- 2*. Sporangiospores ellipsoidal or ovate 5
3. Sporangiospores 8–11 μm diam, brownish, punctulate 3. *C. fuscus*
- 3*. Sporangiospores 3–8 μm diam 4
4. Sporangiospores 5–8 μm diam, chlamydosporae abundant 8. *C. sphaerosporus*
- 4*. Sporangiospores 3–6 μm diam, chlamydosporae absent 5. *C. janssenii*
5. Sporangiospores 6–10 \times 4–7 μm , chlamydosporae abundant ... 7. *C. racemosus*
- 5*. Sporangiospores 4–9 \times 2.5–6 μm , chlamydosporae absent 6

6. Azygospores present in monosporangial cultures .. 1. *C. bainieri*
6*. Azygospores absent7
7. Colonies velvety, low 9. *C. zonatus*
7*. Colonies lanose, not low8
8. Colonies grey, sporangiophores up to 9 μm broad
..... 4. *C. griseo-cyaneus*
8*. Colonies brownish, sporangiophores 12—16 μm broad
..... 2. *C. circinelloides*

List of species

1. *Circinomucor bainieri* (MEHROTRA & BAIJAL) v. ARX, comb. nov.
= *Mucor bainieri* MEHROTRA & BAIJAL. — Aliso 5: 237 (1963).
2. *Circinomucor circinelloides* (van TIEGHEM) v. ARX, comb. nov.
= *Mucor circinelloides* van TIEGHEM. — Anns Sci. nat. 1: 94 (1875).
= *Mucor lusitanicus* BRUDERLEIN.
Further synonyms of this common species have been given by SCHIPPER (1976).
3. *Circinomucor fuscus* (BAINIER) v. ARX, comb. nov.
= *Mucor fuscus* BAINIER. — Bull. Soc. mycol. Fr. 19: 165 (1903).
For synonyms see SCHIPPER (1976).
4. *Circinomucor griseo-cyanus* (HAGEM) v. ARX, comb. nov.
= *Mucor griseo-cyaneus* HAGEM. — Unters. Norweg. Mucorineen 1: 38 (1908).
5. *Circinomucor janssenii* (LENDNER) v. ARX, comb. nov.
= *Mucor janssenii* LENDNER. — Mat. Flor. Crypt. Suisse 3: 88 (1908).
6. *Circinomucor plumbeus* (BON.) v. ARX, comb. nov.
= *Mucor plumbeus* BON. — Abh. naturf. Ges. Halle 8: 109 (1864).
For synonyms see SCHIPPER (1976).
7. *Circinomucor racemosus* (FRES.) v. ARX, comb. nov.
= *Mucor racemosus* FRES. — Beitr. Mykol. 1: 12 (1950).
For synonyms see SCHIPPER (1976).
8. *Circinomucor sphaerosporus* (HAGEM) v. ARX, comb. nov.
= *Mucor sphaerosporus* HAGEM. — Unters. Norweg. Mucorineen 1: 22 (1908).
For other synonyms see SCHIPPER (1976). The species is variable in the size of sporangia and spores. — *Mucor falcatus* SCHIPPER [Antonie van Leeuwenhoek 33: 195 (1967)] is very close, probably identical.
9. *Circinomucor zonatus* (MILKO) v. ARX, comb. nov.
= *Mucor zonatus* MILKO. — Nov. syst. nizsh. Rast. p. 154 (1967).

The species of this genus have been treated in detail by SCHIPPER (1976). Some of the species accepted here are considered to represent

formae of *C. circinelloides* or *C. racemosus*, but can easily be recognized by morphological characters, e. g. by the shape of the sporangiospores.

4. Micromucor (W. GAMS) v. ARX, gen. nov.

Mortierella subgen. *Micromucor* W. GAMS. — Persoonia 9: 381 (1977).

Type species: *M. ramannianus* (MÖLLER) v. ARX

Colonies light, white, vinaceous or ochraceous, velvety, low; sporangiophores erect, at the base often branched; sporangia spherical, up to 25 μm diam, with a small or indistinct columella; sporangiospores small, subspherical or ellipsoidal, hyaline; zygospores unknown; soil borne.

Key to the species

1. Colonies ochraceous, sporangiospores slightly angular, 2—3 μm diam 1. *M. isabellinus*
- 1*. Colonies vinaceous, pink or white 2
2. Chlamydospores abundant, small columellae present 3. *M. ramannianus*
- 2*. Chlamydospores absent or scarce, columellae indistinct 2. *M. longicollis*

List of species

1. *Micromucor isabellinus* (OUDEM.) v. ARX, comb. nov.
= *Mortierella isabellina* OUDEM. — Archs néerl. Sci. (Sér. 2) 7: 176 (1902).
2. *Micromucor longicollis* (DIXON-STEWART) v. ARX, comb. nov.
= *Mortierella longicollis* DIXON-STEWART. — Trans. Br. mycol. Soc. 17: 214 (1932).
3. *Micromucor ramannianus* (MÖLLER) v. ARX, comb. nov.
= *Mucor ramannianus* MÖLLER. — Z. Forst.- u. Jagdw. 35: 321 (1907).
= *Mortierella ramanniana* (MÖLLER) LINNEMANN.

5. Umbelopsis AMOS & BARNETT. — Mycologia 58: 805 (1966).

Type species: *U. versiformis* AMOS & BARNETT

= *U. nana* (LINNEMANN) v. ARX

Colonies restricted, velvety, white or vinaceous; sporangiophores short, with an ampulliform swelling forming one, two or an umbel of tapering branches each bearing a 1- or many-spored, spherical sporangium; zygospores unknown; soil borne.

Key to the species

1. Colonies white, sporangia hyaline 1. *U. nana*
- 1*. Colonies and sporangia vinaceous 2
2. Sporangia 1-spored 2. *U. roseo-nana*
- 2*. Sporangia many-spored 3. *U. vinacea*

List of species

1. *Umbelopsis nana* (LINNEMANN) v. ARX, comb. nov.
= *Mortierella nana* LINNEMANN. — Mucorineen-Gattung Mortierella, p. 16 (1941).
= *U. versiformis* AMOS & BARNETT.
= *Mortierella alba* MAŃKA & GIERCZAK.
2. *Umbelopsis roseo-nana* (W. GAMS & GLEESON) v. ARX, comb. nov.
= *Mortierella roseo-nana* W. GAMS & GLEESON. — Persoonia 9: 112 (1976).
3. *Umbelopsis vinacea* (DIXON-STEWART) v. ARX, comb. nov.
= *Mortierella vinacea* DIXON-STEWART. — Trans. Br. mycol. Soc. 17: 213 (1932).
= *Umbelopsis multispora* WATANABE. — Trans. mycol. Soc. Japan 18: 244 (1977).

Umbelopsis tentatively is placed in the Mucoraceae, because it may be close to *Micromucor*. Its classification in the Thamnidiaaceae, however, can be more justified.

6. *Gilbertella* HESSELTINE. — Bull. Torrey bot. Club 87: 24 (1960).

Type species: *G. persicaria* (EDDY) HESSELTINE

= *Choanephora persicaria* EDDY. — Phytopathology 15: 610 (1925).

Colonies lanose, becoming dark; suspensors swollen, equal, opposite; zygospores subspherical or short cylindrical, brown, thick walled, with conical protuberances; sporangiophores erect, usually unbranched; sporangia spherical, columellate, with a persistent wall, at maturity splitting into equal halves; sporangiospores striate, with hair-like, polar appendages; heterothallic; on plants.

Gilbertella persicaria (EDDY) HESSELTINE has mainly been isolated from rotting peaches, but also from other fruits and from soil. The fungus often has been compared with *Choanephora cucurbitarum* (BERK. & RAV.) THAXTER and *Ch. trispora* (THAXTER) SINHA. In *Choanephora* species the sporangiospores (and conidia) are similar to those of *Gilbertella persicaria*; the smooth zygospores with apposite suspensors however are very different.

7. *Rhizomucor* (LUCET & COST.) VUILL. — Encycl. Mycol. 2: 41 (1931)

Mucor sect. *Rhizomucor* LUCET & COST. — Compt. Rend. hebd. Séanc. Acad. Sci. 129: 1033 (1899).

Type species: *Rh. parasiticus* LUCET & COST.

= *Mucor pusillus* LINDT.

= *Rh. pusillus* (LINDT) SCHIPPER.

Colonies expanding, lanose, greyish; hyphae often forming rhizoids; suspensors formed on aerial hyphae, equal, opposite; zygospores spherical or nearly so, brown or black, covered with wart-like

projections; sporangiophores erect, branched; sporangia terminal, spherical, pigmented, with an obovate columella and a deliquescent wall; sporangiospores small, spherical or nearly so; thermophilic; homothallic or heterothallic; soil borne.

SCHIPPER (1978) distinguished three species. *Rh. pusillus* is a common species, it may be homothallic or heterothallic, and the zygospores have a diameter of 50—80 μm . *Rh. michei* (COONEY & EMERSON) SCHIPPER is homothallic and can be distinguished from *Rh. pusillus* by smaller zygospores. *Rh. tauricus* (MILKO & SCHKURENKO) SCHIPPER is known by a single strain and can hardly be distinguished from *Rh. pusillus*.

The presence of rhizoids and other characters suggest a relationship to *Rhizopus*.

8. **Parasitella** BAINIER. — Bull. Soc. mycol. Fr. 19: 153 (1903).

Type species: *P. simplex* BAINIER

= *P. parasitica* (BAINIER) SYD.

P. parasitica, the only species of the genus, is mycoparasitic on other Mucorales, heterothallic and differs from all other Mucoraceae by the suspensors, which form finger-like outgrowths. The zygospores are brown and have conical or spine-like projections. The columellae of the deliquescent sporangia are spherical, the sporangiospores ellipsoidal.

Parasitella seems to be closer to *Circinomucor* than to other genera of the Mucoraceae.

B. Genera to be classified in other families

If the above given definition of the Mucoraceae is accepted, several genera have to be excluded from the Mucoraceae sensu lato. This is preferable, because the genera of the Mucoraceae sensu stricto are closer to *Cunninghamella*, *Thamnidium* and other Thamnidiaceae than to genera such as *Absidia*, *Rhizopus* or *Phycomyces*, hitherto classified in Mucoraceae. These genera have to be classified in 2 separate families:

1. **Absidiaceae** v. ARX, fam. nov.

Coloniae celeriter crescunt, stolones et rhizoidea saepe formans; suspensores inflati, aequalis et oppositi; zygosporae globosae, nudaе vel appendices suspensores circumcinctae; sporangiophora erecta, non ramosa, saepe in umbellas, apicalibus apophyse; sporangia globosa, obovata vel clavata; columellae conicae; sporae unicellularis, hyalinae vel coloratae, leves vel striatae.

Genus typicum: *Absidia* van TIEGHEM.

Colonies fast growing; hyphae often forming stolons and rhizoids; suspensors swollen, usually equal and opposite; zygospores spherical

or nearly so, usually dark brown, smooth, pitted, furrowed or covered with irregular protuberances, naked or more often surrounded by hypha-like appendages of the suspensors; sporangiophores usually erect, simple or slightly branched, often in umbels on a common base, apically with a funnel-shaped or swollen apophysis; sporangia spherical, obovate or broadly clavate, often with a conical columella and a deliquescent wall; sporangiospores 1-celled, hyaline or slightly pigmented, smooth, striate or punctulate.

Type genus: *Absidia* van TIEGHEM.

The following genera have to be classified in the Absidiaceae: *Absidia* van TIEGHEM; *Actinomucor* SCHOSTAK.; *Amylomyces* CALMETTE sensu ELLIS & al., 1976; *Chlamydoabsidia* HESSELTINE & J. ELLIS; *Circinella* van TIEGHEM & Le MONNIER; *Dicranophora* SCHRÖTER; *Gongronella* RIBALDI; *Halteromyces* SHIPTON & SCHIPPER; *Pirella* BAINIER; *Rhizopodopsis* BOEDIJN; *Rhizopus* EHRENB. (including *Thermomucor* SUBRAHAMANYAM & al.); *Sporodiniella* BOEDIJN; and *Syzygites* EHRENB.

Keys to the genera are given by O'DONNELL (1979) and v. ARX (1981).

The Absidiaceae are close to genera such as *Radiomyces* EMBREE or *Thamnostylum* v. ARX & UPADYHAY, which have zygospores similar to those of *Absidia* or *Rhizopus*. Stolons also are present and the ovate or clavate sporangia are apophysate.

2. *Phycomycetaceae* v. ARX, fam. nov.

Coloniae celeriter crescunt, sine distinctis stolones; suspensores recurvi, forcepiformes, oppositi, verrucis ramosis, spinosis, saepe zygotam cingentem; zygosporae doliiformes, pallidae, leves, foveatae vel striatae; sporangiophora erecta, non ramosa, plerumque longior quam 50 mm; sporangia magna, globosa, atrata, cum vel sine aphophysibus, saepe metallico fulgore; sporae ellipsoideae vel globosae, leves, hyalinae, magnae.

Genus typicum: *Phycomyces* KUNZE.

Colonies fast growing, without distinct stolons, suspensors recurved, tong-like, opposite, with branched, spiny outgrowths often surrounding the zygote; zygosporae barrel-shaped, light, smooth, pitted or striate; sporangiophores erect, unbranched, usually longer than 50 mm (in *Spinellus* shorter); sporangia spherical, dark, with or without apophysis, large, often with a metallic lustre; sporangiospores ellipsoidal-fusiform or spherical, smooth, hyaline, often large.

Type genus: *Phycomyces* KUNZE.

This family comprises the genera *Phycomyces* KUNZE and *Spinellus* van TIEGHEM. Typical species of the former genus with very long sporangiophores are *Ph. nitens* KUNZE, *Ph. microsporus* van TIEGHEM

and *Ph. blakesleeanus* BURGEFF, all coprophilous and rather rare. *Spinellus fusiger* (LINK) van TIEGHEM grows on mushrooms and is unknown in pure culture. *Phycomycès agaricola* BOEDIJN [Sydowia 12: 335 (1958)], also found on agarics, may be identical to *S. fusiger*. Some more species have been described (ZYCHA & SIEPMANN, 1969).

3. Mortierellaceae A. FISCHER

Colonies expanding, usually lanose, white or light greyish, with a garlic odour; hyphae rather thin-walled and delicate, often forming an abundant aerial mycelium; suspensors equal or unequal, often parallel, apposite; zygospores roundish or polyhedral, thick-walled, smooth, hyaline, naked or embedded in a hyphal envelope; sporangio-phores simple or branched, often tapering, apically forming spherical or sausage-shaped sporangia without distinct columella, 1- or many-spored; sporangiospores spherical, polyhedral or ellipsoidal; chlamydo-spores often present, hyaline, smooth or with projections, thin walled.

Type genus: *Mortierella* COEMANS.

The zygospores are rather similar to those of *Choanephora* CURREY (Choanephoraceae), *Pilobolus* TODE (ex FR.) and *Pilaira* van TIEGHEM (Pilobolaceae) and *Piptocephalis* de BARY and *Syncephalis* van TIEGHEM & Le MONNIER (Piptocephalidaceae).

The Mortierellaceae contain mainly the genus *Mortierella* (including *Azygozygum* CHESTERS and *Haplosporangium* THAXTER) with nearly 70 mainly soil borne species (GAMS 1976, 1977; BENJAMIN, 1978; O'DONNELL, 1979).

The genus *Echinosporangium* MALLOCH (1967) is well characterized by sausage-shaped, at the ends spiny sporangia. Its type species *E. transversalis* MALLOCH is known by a single strain.

4. Thamniaceae, Cunninghamellaceae and Radiomycetaceae

The Thamniaceae BREFELD contain a rather large number of genera (BENNY & BENJAMIN 1975, 1976). Species of the genera *Backusella* J. ELLIS & HESSELTINE, *Thamnidium* LINK, *Cokeromyces* SHANOR, *Ellisiomyces* BENNY & R. K. BENJAMIN, *Chaetocladium* FRES., *Benjaminiella* v. ARX and *Mycotypha* FENNER have black, spiny zygospores, similar to those of *Zygorhynchus* species. The suspensors are equal or nearly so and opposite. The species of *Thamnostylum* v. ARX & UPADHYAY differ by the formation of stolons and by larger zygospores, similar to those of *Rhizopus*.

The Radiomycetaceae HESSELTINE & J. ELLIS contain the genera *Radiomyces* EMBREE and *Hesseltinella* UPADHYAY, both possess stolons and rhizoids. Zygospores are known only in *Radiomyces* and

are surrounded by outgrowths of the suspensors. The sporangiospores are small, often rod-shaped.

The Cunninghamellaceae NAUMOV now are restricted to the genera *Cunninghamella* MATRUCHOT and *Thamnocephalis* BLAKESLEE. The family is characterized by 1-spored, echinulate sporangia (conidia) borne on swellings of erect, long, branched sporangiophores and by bright, usually orange zygospores with opposite suspensors.

C. Key to the families of Mucorales

1. Suspensors (gametangia) recurved, tong-like, forming branched, spiny projections; zygospores barrel-shaped, smooth or nearly so, sporangiophores unbranched, often very long and with a metallic lustre; coprophilous or on agarics ... Phycomycetaceae
- 1*. Above characters not combined 2
2. Suspensors apposed; zygospores hyaline, smooth, naked or covered by branched hyphae; colonies light, lanose, with a garlic odour; sporangia not columellate, without apophysis; usually soil-borne Mortierellaceae
- 2*. Above characters not combined 3
3. Sporangiospores pigmented, with polar, hair-like appendages or striate; sporangial wall splitting into halves; suspensors apposite Choanephoraceae
- 3*. Above characters not combined 4
4. Sporangial wall cutinized above; suspensors apposite, tong-like Pilobolaceae
- 4*. Sporangial wall not cutinized above, suspensors opposite 5
5. Sporangia 1-spored, conidium-like, spiny, formed on swellings, with short stalks; sporangiophores erect, with lateral branches; zygospores orange, often spiny Cunninghamellaceae
- 5*. Above characters not combined 6
6. Sporangia cylindrical, sporangiospores in rows Syncephalastraceae
- 6*. Sporangia not cylindrical, sporangiospores not in rows 7
7. All sporangia alike, usually with a distinct columella, rarely 1-spored 8
- 7*. Sporangia not alike, at least partly without columella and formed on erect, much branched sporangiophores 9
8. Zygospores naked, with a wall ornamented with spines, warts or projections; sporangia spherical, not apophysate ... Mucoraceae
- 8*. Zygospores naked or covered with outgrowths of the suspensors, smooth or verrucose; sporangia obovate-clavate or spherical, usually apophysate Absidiaceae

9. Sporangiohores apically umbellate; sporangia formed on swellings; sporangiospores small, often rod-shaped Radiomycetaceae
.....
9*. Above characters not combined Thamniaceae

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