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Zygospore formation in *Mortierella capitata*

Yousuke Degawa and Seiji Tokumasu

Sugadaira Montane Research Center, University of Tsukuba, Sanada, Nagano 386–22, Japan

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A novel type of zygospore formation is described in the heterothallic species *Mortierella capitata*, which was repeatedly isolated from soils inhabited by pillbugs (*Armadillidium vulgare*, Isopoda). Zygospore formation was induced on media containing sterilized arthropods. Anisogamy and colorless zygospore walls are shared with other zygosporic species of *Mortierella*, but a unique feature of *M. capitata* is the production of zygospores on elongated macrosuspensors which are covered by branches of the microsuspensors. This kind of zygosporogenesis is termed "capitata-type" here. The taxonomic position of *M. capitata* is discussed based on the zygospore characteristics.

Key Words——*Actinomortierella*; anisogamy; capitata-type; Isopoda; Mucorales.

In the family Mortierellaceae, zygospore morphology has never been adopted as a taxonomic criterion for distinguishing infrafamilial taxa due to insufficient information. Benjamin (1978), reviewing the history of the family, noted that the utility of zygospore characteristics in classification could be assessed only after much additional studies on zygospores. Only for the genus *Gongronella*, which was thought to belong to the Mortierellaceae by the author of the genus (Ribaldi, 1952; Chalabuda, 1973), do its typical mucoralean zygosporic characteristics warrant classification in the Mucoraceae (Hesseltine and Ellis, 1964). The characterization of the family Mortierellaceae is based entirely on asexual characteristics, because zygospores have been recorded for only 20 species of *Mortierella*. Gams (1977) divided the genus into two subgenera, *Micromucor* and *Mortierella*, and distinguished nine sections in the latter, viz. *Actinomortierella*, *Alpina*, *Haplosporangium*, *Hygrophila*, *Mortierella*, *Schmuckeri*, *Simplex*, *Spinosa*, and *Stylospora*, based on branching patterns of the sporangiophores. Among these ten taxa, zygospores have been found neither in the subgenus *Micromucor* nor in the three sections *Actinomortierella*, *Haplosporangium* and *Schmuckeri*.

Mortierella vesiculosa B. S. Mehrotra, Baijal & B. R. Mehrotra was described from India (Mehrotra et al., 1963). Embree (1963) reported it from England and suggested its possible conspecificity with *Mortierella capitata* Marchal. *Mortierella vesiculosa* is now generally regarded as a synonym of *M. capitata* (Linnemann, 1969; Mil'ko, 1974; Gams, 1977). Chalabuda (1968) designated it (as *M. vesiculosa*) as the type of the genus *Actinomortierella*. Gams (1977) relegated this to section *Actinomortierella* in the genus *Mortierella* together with *Mortierella ambigua* B. S. Mehrotra.

Terms used in the present paper as "zygospore" and "zygosporangium," and those for describing zygosporogenesis follow Ansell and Young (1983), and Edelmann and Klomparens (1995) with slight exceptions. Ansell and Young (1983) called the structure within a zygosporangium the "zygospore proper" to distinguish it from the vaguer term "zygospore." The entire structure between two suspensors is a "zygosporangium," the outermost wall of which is a continuation of the gametangial wall.

Materials and Methods

Isolation Soil samples were collected from fields where pillbugs (*Armadillidium vulgare* (Latreille), Isopoda) were numerous. The samples were kept moist in plastic sample cups, 101 mm diam × 44 mm height, at room temperature. When needed, sterilized dried shrimps (*Sergestes lucens* Hansen, Decapoda) were put on the soil surface as baits. Under a stereomicroscope the samples were screened for the presence of sporangiophores of *M. capitata* and sporangia were picked off. Isolates from single sporangiospores were established, using a Skerman type micromanipulator, on Miura's medium (LcA: basic nutrient-salt solution agar for lignin cellulose agar) (Miura and Kudo, 1970).

The isolates examined were: DM 160 (mating type =MTA), from garden soil, Gunma, in Nov. 1992 (deposited in CBS as CBS 293.96); DM 161 (MTB), from garden soil at the campus of Shinshu Univ., Ueda, Nagano, in Jul. 1993, the locality indicated by Indoh and Kudo (1967), (deposited in CBS as CBS 294.96); DM 410 (MTA), from garden soil at campus of Kyoto Univ., Kyoto, in Mar. 1994; DM 343 (MTA), from soil at Wakayamajo castle, Wakayama, in Jul. 1994; DM 96 (MTB), from soil under a hedge, Kashihara, Nara, in Sept. 1994; DM 138 (MTB), from garden soil, Yokohama, Kanagawa, in Oct. 1994. Identification of the isolates was based on cultures grown on LcA for 7 d at 20°C.

Mating Two mycelial discs (5 mm in diam) punched out from the periphery of growing colonies on LcA were inoculated on 0.3% shrimp agar plates (ShA; 3.0 g dried

ground shrimps, *S. lucens*, 15.0 g agar per 1.0 L distilled water) 10 mm apart from each other and incubated at 5, 10, 15, 20, 25, 30 and 35°C. Czapek solution agar plates (CzA; Difco, sucrose and minerals autoclaved together) were also prepared, on which sterile pieces of arthropods were placed for the observation of zygosporogenesis on a natural substrate. Two mycelial discs were inoculated 20 mm apart from each other and autoclaved, then dead isopods (*A. vulgare* or *Porcellio scaber* Latreille) or shrimps were placed between the discs. The plates were incubated at 20°C.

Light microscopy Serial observations of zygospore development were carried out from the reverse side of plastic Petri dish cultures. Micrographs were taken at ca. 0.5–1 h intervals, using a microscope (Zeiss Axioskop) equipped with Nomarski differential interference contrast optics (DIC). The samples were mounted in 90% lactic acid and stained with cotton blue or aniline blue when needed. Measurements were made on living materials on ShA or on mounted slides.

Scanning electron microscopy According to a procedure modified after Ansell and Young (1983), zygospores taken from the surface of ShA were fixed in 3% glutaraldehyde in 0.1 M sodium cacodylate buffer at 4°C for 5 h, washed in the buffer and distilled water, then dehydrated through an ethanol series. The specimens were then dried with a critical-point dryer (model CP-5A, Topcon) in liquid CO_2 and coated in an ion sputter (JFC-1100, JEOL). Observation was carried out using a scanning electron microscope (JSM T-200, JEOL) operating at 5 to 15 kV.

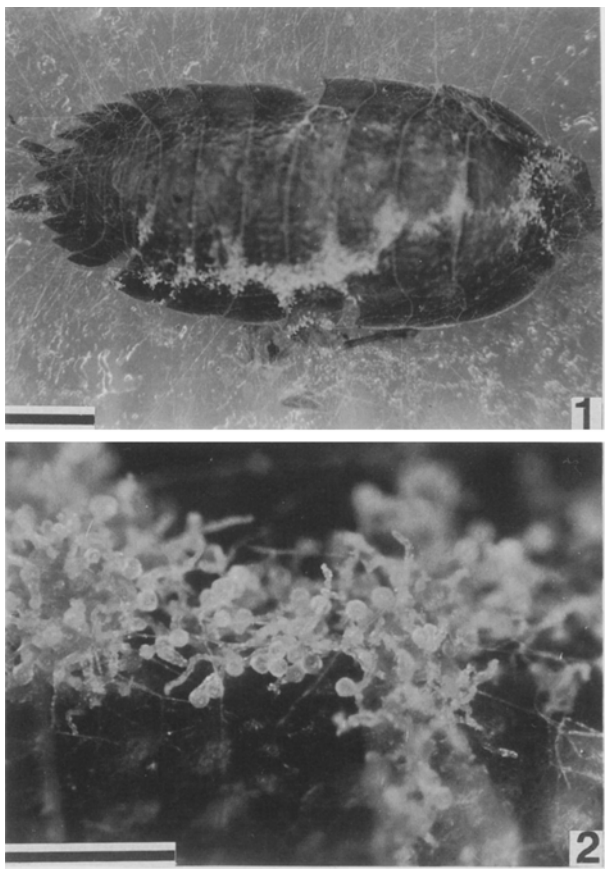
Results

An isolate of *M. capitata* was recovered by the present authors in 1993 from soil in the campus of Shinshu Univ., Ueda, Nagano, the same place where Indoh and Kudo (1967) had obtained the same species under the name of *M. vesiculosa*. The soil of both samples was densely inhabited by pillbugs (*Armadillidium* sp., Isopoda). Unfortunately, the isolate by Indoh and Kudo has been lost, but several additional isolates of the same species have recently been recovered from soil taken from similar habitats in different parts of Japan. We succeeded in inducing zygospore formation by placing sterilized arthropod bodies on the culture media.

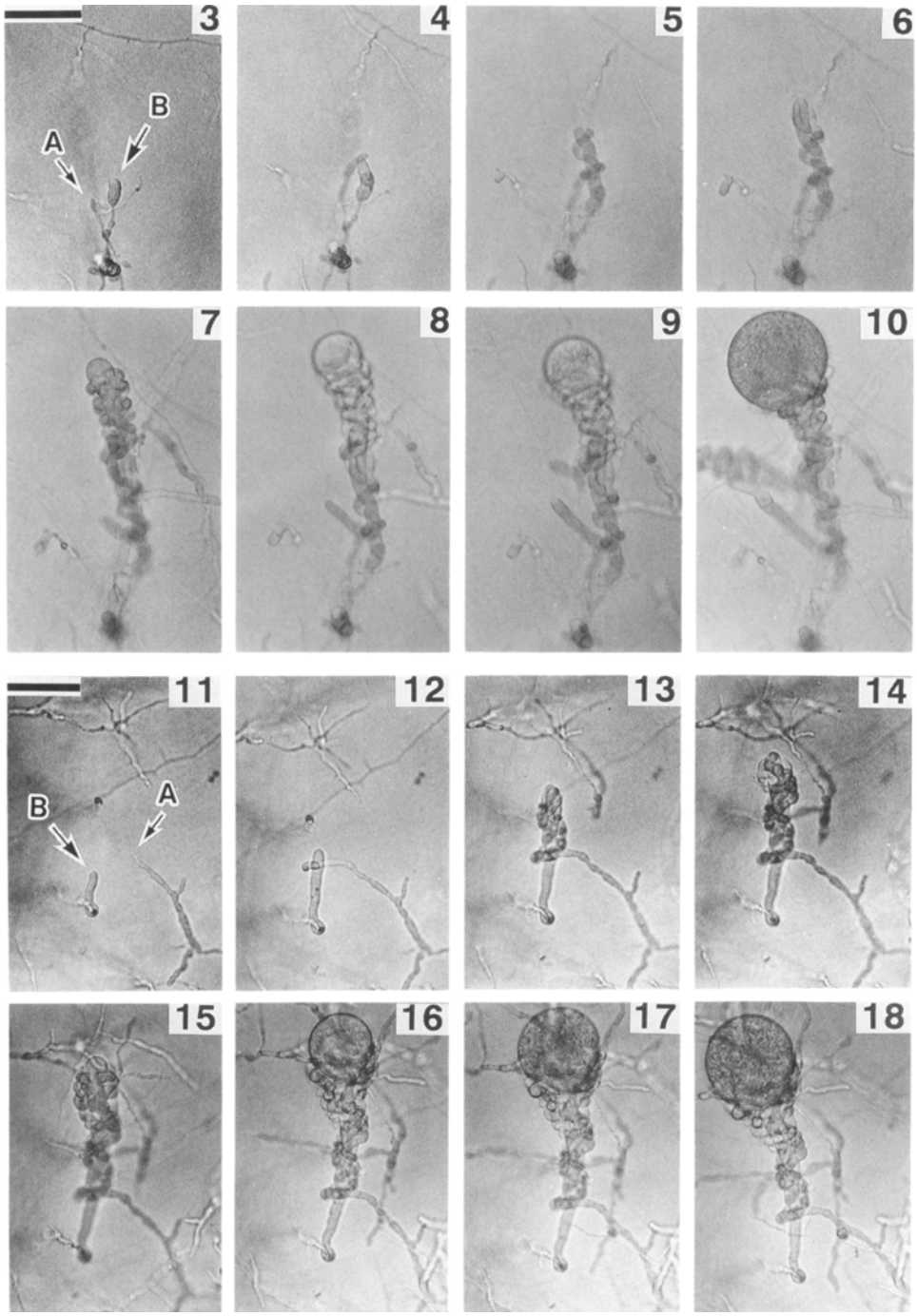
Identification The identification of the isolates was based on Linnemann (1969) and Gams (1977). The numerous narrow branches arising from an inflation beneath the terminal sporangium and the formation of globose sporangiospores are characteristic of *M. capitata*.

Mating When heterothallism was established between two isolates of the present species on agar plates, the mating types were arbitrarily designated as A and B. Each isolate reacted as one of the mating types. Zygospore formation occurred at temperatures ranging from 10 to 25°C on arthropods on CzA and on ShA. The temperature optimum lay between 15 and 20°C, where the greatest density of mature zygospores appeared within 1 wk. Zygospores were produced both on the surface and within the agar medium. On plain CzA plates, zygospore formation was never observed. But, in spite of problems noticed with this medium (Gams and Williams, 1963), zygospores were obtained on it after the addition of arthropods. They were seen concentrated on the animal body (Fig. 1). The zygospores appeared on erect fascicles on the surface and also buried inside the animals (Fig. 2). The amount of zygospore production varied depending on the combinations of the isolates. The strongly reacting pair DM 160 (A)–DM 161 (B) produced up to about 1,000 zygospores on ShA in a 9-cm Petri dish at 20°C within 2 wk. Incomplete maturation or bursting of zygospores was often observed.

Zygosporogenesis Morphological observations were carried out for the best mating pair, DM 160 (A) and DM 161 (B), on ShA at 20°C. Two sets of serial micrographs were recorded (Figs. 3–10 and 11–18, respectively). About 1 d after the mycelia of the two strains made contact, several tips of the vegetative hyphae began



Figs. 1, 2. Zygospore formation of *Mortierella capitata* on sterilized isopod (*Porcellio scaber*) placed between the mycelia of both mating types on CzA at 20°C for 1 wk.
1. White line of zygospore mass produced on the isopod. Bar = 2 mm. 2. Magnified part of zygospore mass line. Cylindrical gametangial complex and zygospores with macrosuspensors on the surface of the isopod. Bar = 500 μm.



Figs. 3–10, 11–18. Time-lapse micrographs of initial stages of zygosporogenesis in *Mortierella capitata* on a ShA plate. Bars = 50 μm; A = mating type A; B = mating type B. (Figures in parentheses indicate the time after the stage of Figs. 3, 11, respectively).

3. Two hyphal tips start swelling to form progametangia, the thick one belongs to mycelium of mating type B (right), the thinner one to mating type A (left) (0 h). 4. Contact of two progametangial apices in parallel position (9 h). 5, 6. Initial spiral coiling of two progametangia (13 h, 16.5 h). 7, 8. The microprogametangium starts entwining around the macroprogametangium and branching. The macroprogametangium at the basal part forms a branch on the left side (25.5 h, 28.5 h). 9. The apex of the macroprogametangium swells to form a rounded head (32.5 h). 10. Strongly swollen spherical macrogametangium supported by a macrosuspensor with microprogametangial hyphal branches (41.5 h).

11. Two swollen hyphal tips from a mycelium of mating type A (right) and one of mating type B (left) (0 h). 12. Contact of hyphal apices in perpendicular position (4.5 h). 13, 14. Initial spiral coiling of two progametangia with slight branching (9.5 h, 13 h). 15, 16. The apex of macroprogametangium swells to form a rounded head (16.5 h, 25.5 h). 17, 18. Swollen macrogametangium (28.5 h, 32.5 h).

swelling to produce progametangia (Figs. 3, 11). These tips sometimes branched to connect with other progametangial tips. The hyphal tips from mycelium of mating type B were always larger than those of A. This was the same for all isolates examined. They contacted each other in parallel (Figs. 3, 4) or perpendicular positions (Figs. 11, 12). While the straight thick hyphal tips with a diameter of 8–11 μm elongated, thinner hyphal ends (2–5 μm wide) began coiling around the other suspensor (Figs. 5, 6, 13, 14, 19). At this stage, thick hyphal tips of mating type B were interpreted as macroprogametangia and the thinner ones of mating type A as microprogametangia. The microprogametangia branched frequently (Figs. 7, 13, 14) and entwined densely around the macroprogametangia. The macroprogametangia grew to varying lengths, reaching up to 200 μm. When elongation stopped, the apices gradually swelled to form spherical heads (Figs. 7–9, 15, 16). At the base of the spherical head, a macrogametangial septum was produced to delimit the macrogametangium from the rest, which remained as the macrosuspensor (Fig. 20). On the other hand, the apices of the microprogametangia produced a number of branches that surrounded the lower part of the spherical heads (Figs. 9, 10, 16–18). These branches continued to branch dichotomously (Figs. 28, 29). In the microprogametangia, several septa were recognized, but the main microgametangial septum could not be clearly recognized, since the point of gametangial fusion could not be confirmed yet. The macrogametangia continued to swell up to ca. 60 μm in diam (Figs. 10, 18, 21).

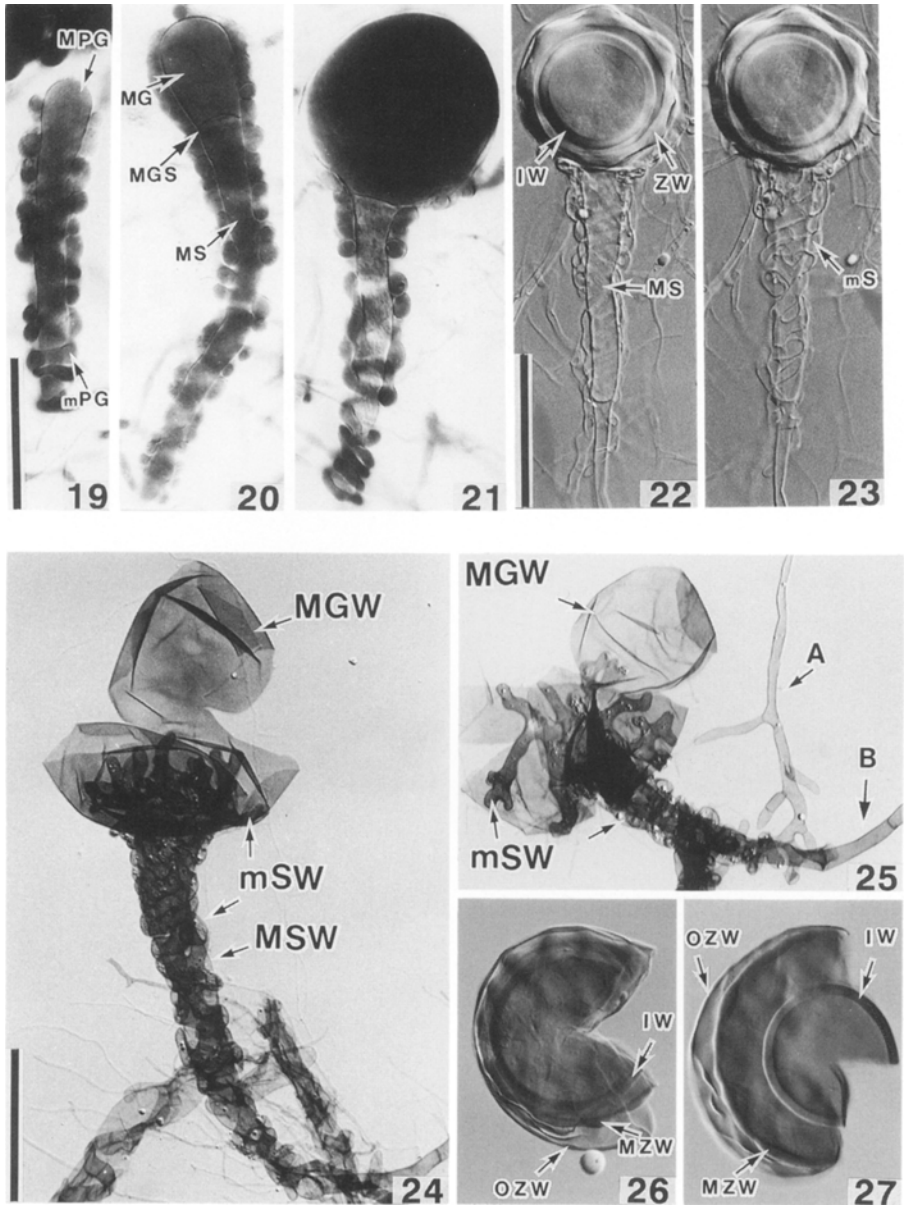
At maturity, the macrosuspensor became evacuated (Fig. 22). The microprogametangium also lost its contents to become a microsuspensor (Fig. 23). The mature macrogametangium was converted into a zygospore, in which two thick walls formed de novo were visible: an undulate wall of the "zygospore proper" (ZW) and a smooth inner wall (IW) lining the cytoplasm (Figs. 22, 23). In scanning electron micrographs, the surface of the mature zygospore (=macrogametangium) showed a honey-comb-like appearance with prominent polygonal ribs (Figs. 28–30). When the mature zygospore was crushed, the "zygospore proper" (Figs. 26, 27) was liberated through the smooth-surfaced macrogametangial wall (MGW in Figs. 24, 25). The thin hull (MGW) is equivalent to the wall of the "zygosporangium." The "zygospore proper" wall consists of the ZW and the IW. The ZW is composed of at least two layers, a thin outer zygospore wall layer (OZW) and a thick and undulate, middle zygospore wall layer (MZW) (Figs. 26, 27).

Discussion

Heterothallism has been reported for thirteen species in the genus *Mortierella*, all of which were anisogamous. The mating system of *M. capitata* is regarded as a rare case of morphological heterothallism. The macroprogametangia and the microprogametangia were consistently produced on mating types B and A, respectively. However, a relation between mating type and gametangial size was demonstrated only once by Gams and Williams (1963), who assumed morphological heterothallism for *Mortierella parvispora* Linnemann. Gams et al. (1972), however, demonstrated physiological heterothallism for *Mortierella elongata* Linnemann, where either mating type could produce macro- and microgametangia depending on the position of the mating points within the mycelium. In the remaining species, no such relationship has yet been confirmed, because the very thin entwining sexual hyphae often cannot be traced back to one of the partners. In *M. capitata*, however, their origin could be traced without difficulty, due to the larger size and different shape of macroprogametangia compared with microprogametangia. Both types of progametangia were comparatively distinct from each other from their initial stages, and the macroprogametangia remained straight for a sufficiently long period (Figs. 3, 11, 25).

Mating of compatible strains was always required to induce zygospores in *M. capitata*. Zygospores did not mature without the appearance of entwining microprogametangial hyphal branches around the macroprogametangium. A cytoplasmic translocation into the zygospore is suggested by the observation that the microprogametangial area became completely evacuated at maturation of the zygospore. Some part of the hyphal branches is likely to function as a microgametangium, though its exact localization could not be found. Thus, we consider that the whole hyphal structure entwining the macroprogametangium functions as a microprogametangium in the initial stage of gametangial development, and functions as a microsuspensor in the mature stage (cf. Ansell and Young, 1983). The possibility remains that *M. capitata* produces azygospores exclusively, because the fusion wall and its breakdown could not be confirmed. Further cytological and ultrastructural investigations might help to resolve this problem.

The remarkable anisogamy and the hyaline zygospore wall appear to be common characteristics of the genus *Mortierella*, and *M. capitata* is not exceptional in these points. The "zygospore proper" is produced endogenously inside the macrogametangial wall (Figs. 24–27) and does not become pigmented at maturity (Figs. 22, 23). In the family Mortierellaceae, zygospores are known only from six sections of *Mortierella* subgenus *Mortierella*. Zygosporogenesis in *M. capitata* differs from that in other sections in several respects. First, the macrosuspensor of *M. capitata* is cylindrical to slightly obconical, whereas that of other species swelled generally more strongly to become tong-like to spherical. Second, the apposed disposition of the suspensors in *M. capitata* is unprecedented. In *Mortierella*, clearly opposed suspensors occur only in the sections *Alpina* (Kuhlman, 1975) and *Stylospora* (Williams et al., 1965; Kuhlman, 1972); in all other sections apposed or half-opposed (tong-like) suspensors were reported (Gams and Williams, 1963; Gams et al., 1972; Kuhlman, 1972; Kuhlman, 1975; Gams and Hooghiemstra, 1976). In several species with half-opposed suspensors, twisting of progametangia was described, which is most conspicuous in *M. parvispora* (Gams and Williams, 1963). But in



Figs. 19–21. DIC micrographs of lactic acid-mounted slides of *Mortierella capitata* zygospores, stained with cotton blue. Bar = 50 μm; MPG = macroprogametangium; mPG = microprogametangium; MG = macrogametangium; MGS = macrogametangial septum; MS = macrosuspensor.

19. Microprogametangial hyphal branches entwining around a macroprogametangium. 20. Macrogametangial septum delimiting the macrogametangium from the macrosuspensor. 21. Spherical macrogametangium containing dense cytoplasm as indicated by strong staining with cotton blue, supported by a macrosuspensor and surrounding microprogametangial hyphal branches.

Figs. 22, 23. DIC micrographs of lactic acid-mounted mature *Mortierella capitata* zygospores, not stained (the same material differently focused).

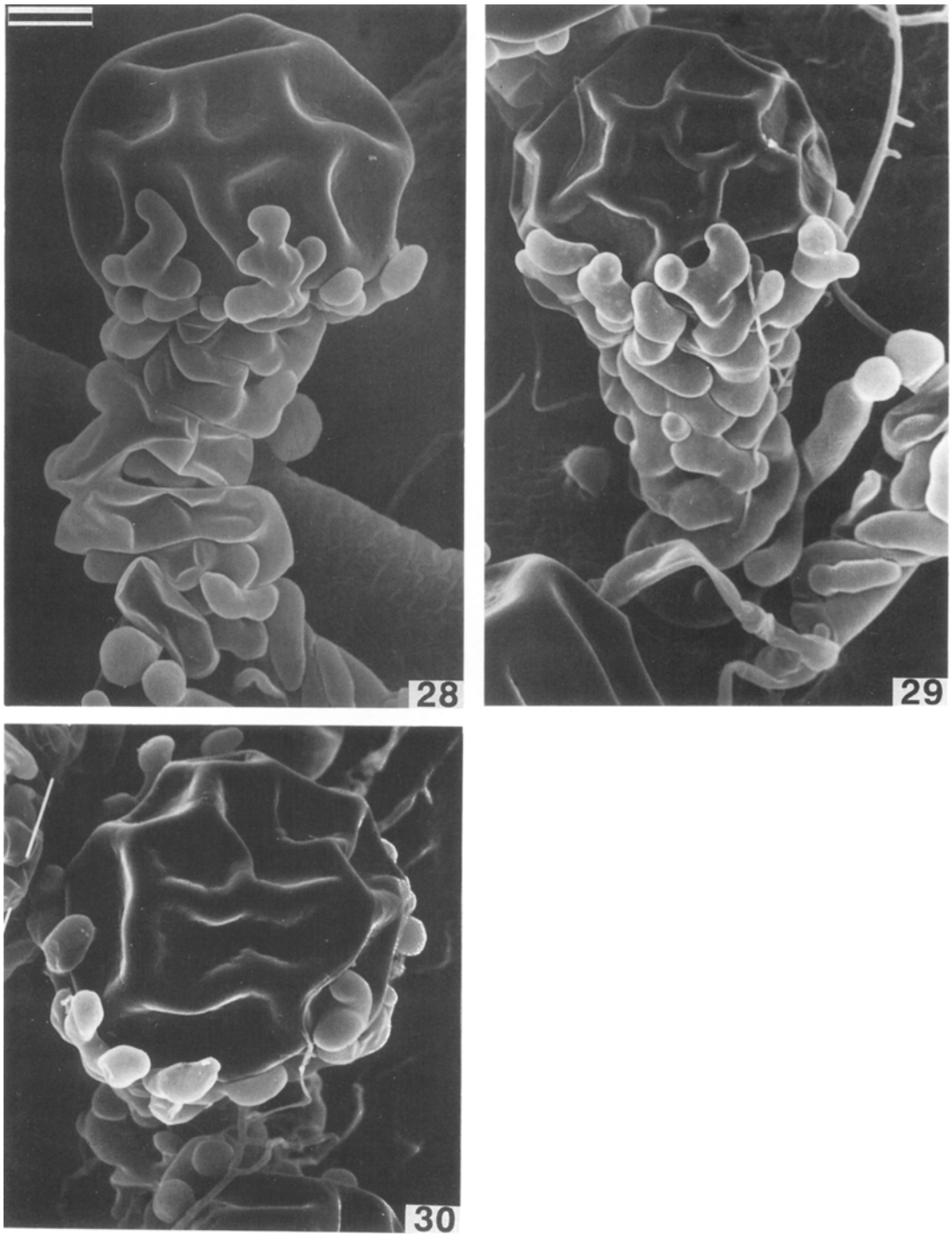
Bar = 50 μm; ZW = zygospore wall; IW = inner wall; MS = macrosuspensor; mS = microsuspensor.

22. Focused on the empty macrosuspensor. Two thick hyaline walls shown within the zygospore, an outer undulate zygospore wall and an inner round wall. 23. Focused on the empty microsuspensor.

Figs. 24–27. DIC micrographs of crushed mature zygospore of *Mortierella capitata*, stained with aniline blue.

Bar = 50 μm. MGW = Macrogametangial wall; mSW = microsuspensor wall; MSW = macrosuspensor wall; OZW = outer thin zygospore wall layer; MZW = middle undulate zygospore wall layer; IW = inner wall; A = mating type A; B = mating type B.

24. Thin layer of macrogametangial wall (= zygosporangial wall), with macrosuspensor and hyphal branches of the microsuspensor. 25. Thin layer of macrogametangial wall with suspensors, viewed from below. Radially extending hyphal tips of microsuspensor dichotomously branched. Origin of the thinner microsuspensor hyphae (from mating type A) with several branches and septa. 26. Crushed zygospore proper, liberated from zygosporangium, showing the zygospore wall (the outer thin layer and thick middle undulate layer) and the inner thick round wall. 27. The inner thick wall detached from zygospore wall layers.



Figs. 28–30. Scanning electron micrographs of mature zygospores of *Mortierella capitata*.
Bar = 10 μm. 28. Honey-comb-like dimpled zygospores, in the lower part surrounded by dichotomously branched apices of microsuspensors. 29. Zygospore with prominent polygonal ribs. 30. Top surface of zygospore surrounded by apices of microsuspensor branches.

that case the twisting is limited to the initial stages, and progametangia are initially almost equal in size. In *M. capitata*, however, the microprogametangia wind around the macroprogametangia, covering rather than intertwining with them.

Lastly, the zygospore of *M. capitata* is partly covered by hyphal branches. Although recently reported zygospores in the genus are naked, zygospores covered with interwoven hyphae are known in several species. For the three species in the sections *Mortierella* and *Simplex*,

Mortierella polycephala Coemans, *M. globulifera* Rostrup and *M. rostafinskii* Brefeld, the hyphae of the sheaths developed independently and did not originate from the progametangia or suspensors (Kuhlman, 1972); these hyphae surrounded the whole surface of the zygospore. In two other species, *Mortierella nigrescens* van Tieghem (van Tieghem, 1876) and *Mortierella indohii* Chien (Chien et al., 1974; Ansell and Young, 1983), hyphae covering the zygospore originated directly from one or both of the suspensors like the appendages of suspensors in the genera *Absidia* and *Phycomyces*. In *M. capitata*, the covering hyphal branches are apparently organized by the microprogametangium itself and surround both the macrosuspensor and the lower portion of the zygospore. Therefore, these hyphal branches are not comparable with the covering hyphae in either of the aforementioned species.

The zygosporic characteristics of *M. capitata* are highly specialized and quite different from those in any other *Mortierella* species. Thus, we propose here the term 'capitata-type' for this type of zygospore formation.

Variations in zygospore morphology mentioned above have not hitherto been used as taxonomic criteria. In his discussion of the hyphal covering of zygospores, Kuhlman (1972) recommended retaining many modifications of zygospores in a wide concept of the genus *Mortierella*, rather than subdividing it into genera on the basis of zygospore types. He pointed out that a grouping of species into types with covered or uncovered zygospores did not correlate with any asexual morphological classification system.

However, the taxonomic position of *M. capitata* has also been debated when only the asexual morphology is considered. To Linnemann (1941) the position of *M. capitata* remained unresolved. Mehrotra (1967) established a new section, *Ambigua*, to include *M. capitata* (=*M. vesiculosa*) with two other species. Although he never validly published this section, Linnemann (1969) followed him. Embree (1963) discussed the possible relationship between the species and the genus *Syncephalis* (Piptocephalidaceae). Indoh and Kudo (1967) suggested that the species exhibits enough asexual morphological features to be placed in a new subgenus or even genus. Chalabuda (1968) proposed a new genus, *Actinomortierella*, based on the asexual characteristics, and the new combination *Actinomortierella vesiculosa* (B. S. Mehrotra, Baijal & B. R. Mehrotra) Chalabuda. Chalabuda (1973) published another Latin diagnosis of the genus additionally including four invalidly published combinations, *Actinomortierella ambigua* (B. S. Mehrotra) Chalabuda, *A. capitata* (Marchal) Chalabuda, *A. umbellata* (Chien) Chalabuda, and *A. wolfii* (Mehrotra & Baijal) Chalabuda. Gams (1970) relegated the group to a section of the genus *Mortierella*, in which he retained only two species. On the other hand, Mil'ko (1974) placed *M. capitata* in section *Polycephala*. These various taxonomic views were all based on different interpretations of the same characteristics of asexual morphology, namely, sporangiophores with a subapical vesicle that bears small lateral branches.

The presently reported 'capitata-type' zygospore formation clearly distinguishes *M. capitata* from all other sections in the subgenus *Mortierella*. This fact and the characteristics of asexual morphology seem to be sufficient to segregate the species as an independent genus in the family Mortierellaceae, viz. *Actinomortierella* Chalabuda. This will require an emendation of the generic definition including sexual features. The classification of the closest relative, *M. ambigua*, in relation to this genus also requires further studies.

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