

Ultrastructural studies on zygomycotan fungi in the Zoopagaceae and Cochlonemataceae

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Received: 5 May 2010 / Accepted: 14 October 2010 / Published online: 18 November 2010
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Abstract The morphology of fungi in the Zoopagaceae and Cochlonemataceae (Zoopagales, Zoopagomycotina, Zygomycota) is reviewed, and some new ultrastructural information is added on conidia and zygospores, as well as haustoria in the former family and vegetative thalli in the latter. The cell wall of the conidia of *Acaulopage dichotoma*, *Ac. tetraceros*, *Stylopage cephalote*, *Zoophagus insidians*, and *Zph. tentaculum* (Zoopagaceae), and of *Cochlonema odontosperma* and *Endocochlus gigas* (Cochlonemataceae), is known to be composed of outer electron-dense and inner less dense layers in ultrathin sections, and no additional cell walls were found on the conidial cell wall. Although two nuclei were found in the zygosporangium before maturation to the zygospore in *Acaulopage raphidospora* (Zoopagaceae), more than one nucleus had never been observed previously in a zygospore in either of these families in ultrathin sections.

Keywords Conidium · *Endocochlus* · *Euryancale* · Haustorium · Zygospore

Introduction

The two fungal families Zoopagaceae and Cochlonemataceae are currently included in the Zoopagales, Zoopagomycotina, Zygomycota, together with three other families: Helicocephalidaceae, Sigmoidomycetaceae, and Piptocephalidaceae (Hibbett et al. 2007). The Zoopagaceae contains *Acaulopage*, *Cystopage*, *Stylopage*, *Zoopage*, and

Zoophagus, whereas the Cochlonemataceae comprises *Amoebophilus*, *Aplectosoma*, *Bdellospora*, *Cochlonema*, *Endocochlus*, and *Euryancale* (Kirk et al. 2008). According to Saikawa (2010), 99 species and six varieties in the two families have been known as parasites of microscopic animals, such as rhizopods, nematodes, and rotifers. However, *Acaulopage tigrina* Ciccarone (Ciccarone 1989) was excluded from those 99 species because the “organism” does not have any vegetative hyphae and vegetative thalli at all.

In the Zoopagaceae, each species captures animals by adhesion of hyphae, penetrates through their pellicle or cuticle, and makes haustoria or infectious hyphae in the host animals to absorb nutrients, although those fungi producing filiform-shaped conidia also capture the animals by such conidia in addition to hyphae (Drechsler 1933, 1935b, 1936, 1947; Jones 1959, 1962). On the other hand, each species in the Cochlonemataceae parasitizes rhizopods or nematodes by conidia that attach to the pellicle of the rhizopods, or that are swallowed by nematodes in species of *Euryancale* (Saikawa and Katsurashima 1993). After germination of conidia at the point of attachment with the animals, vegetative thalli grow in the host, although *Bdellospora helicoides* Drechsler (Drechsler 1935a) and *Amoebophilus* spp. (Dangeard 1910; Miura 1978; Barron 1983) in the Cochlonemataceae produce the haustorium exceptionally as do fungi in the Zoopagaceae. In this study, morphology of fungi in the two families is reviewed at an ultrastructural level, which is supplemented with some new information by electron micrographs.

Materials and methods

Fungi in the Zoopagaceae and Cochlonemataceae used in the present study were recovered from leaf mold

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accumulated on the ground and immediately below the surface of water. The fungus materials, dates, and sites of their collection (country, Japan) and collectors are as follows: *Acaulopage (Ac.) dichotoma* Drechsler (see Fig. 5), 25 February 1994, Koganei, Tokyo, Toru Kadowaki; *Ac. rhabidospora* Drechsler (see Figs. 1, 9–11), September 1988, Koganei, Tokyo, Hajime Makii; *Ac. tetraceros* Drechsler (see Figs. 3, 6), 12 December 1993, Koganei, Tokyo, Toru Kadowaki; *Cochlonema (Co.) odontosperma* Drechsler (see Figs. 17, 20, 21), 10 April 1985, Nibukata, Tokyo, Hiroki Sato; *Endocochlus (En.) gigas* Drechsler (see Figs. 13, 14, 16), 22 September 1994, Shakotan, Hokkaido, Masatoshi Saikawa; *Euryancale (Eur.) marsipoides* Aoki (see Figs. 15, 19, 22), September 1991, Kinosaki, Hyogo, Yuji Aoki; *Eur. saccispora* Drechsler (see Fig. 18), 24 April 1988, Koganei, Tokyo, Yuji Aoki; *Stylopaga (S.) cephalote* Drechsler (see Fig. 2), 9 September 1989, Hachijo-isl, Tokyo, Yuji Aoki; *S. cephalote* (see Fig. 7), 1 December 2006, Koganei, Tokyo, Yuki Masumura; *Zoophagus (Zph.) insidians* Sommerst. (see Fig. 4), 11 December 1996, Koganei, Tokyo, Masao Goho; *Zph. pectosporus* (Drechsler) M.W. Dick (see Fig. 12), April 1988, Takao, Tokyo, Yuka Wakai; *Zph. tentaculum* Karling (see Fig. 8), 11 June, Hinohara, Tokyo, Masatoshi Saikawa.

The samples were put into a plastic bag (0.03 × 130 × 250 mm), turned inside out to prevent touching the sample by hand, and transported in an outer bag. The fungi are found on water agar (WA) plates in Petri dishes 90 mm in diameter containing slightly moist, 10–20 g leaf mold incubated at room temperature (20°–22°C) for 1–2 weeks. During incubation, the Petri dishes were set in a plastic container to maintain humidity. To obtain nonaxenic cultures of the fungi destroying microscopic animals, a block of agar ~7 × 7 mm containing the infected animals was cut with a scalpel and placed on a WA plate. Another block containing only uninfected animals was cut and placed on SAA [=Saikawa and Aoki's agar: KNO₃, 0.2 g; MgSO₄·7H₂O, 0.02 g; KH₂PO₄, 0.1 g; K₂HPO₄, 0.3 g; NaHCO₃, 0.02 g; Na₂SiO₃, 0.02 g; agar, 20 g; distilled water, 1 l (Saikawa and Kadowaki 2002)]. In the case of rotifers, distilled water of the same amount as agar was poured onto the agar plate in every case (1/2 dilution), whereas for rhizopods 1/3-strength SAA was preferable (Hirotani-Akabane and Saikawa 2010). About 7 days after transfer, animals multiplied on SAA at 20°–22°C were added to the WA plates with the fungus. For electron microscopy, specimens were fixed in 3% (v/v) glutaraldehyde buffered with 0.1 M sodium phosphate (pH 7.2) for 1.5 h at room temperature, washed with the same buffer for 1.5 h, and postfixed in OsO₄ in the same buffer at 4°C for 12 h. After dehydration through an acetone series, the fungal materials were embedded in Epon. Ultrathin

sections were stained with uranyl acetate and lead citrate and observed with a JEOL 100CXII electron microscope operating at 80 kV. A Hitachi H-1250M high-voltage electron microscope was also used, operating at 1000 kV, for sections 3–5 μm thick.

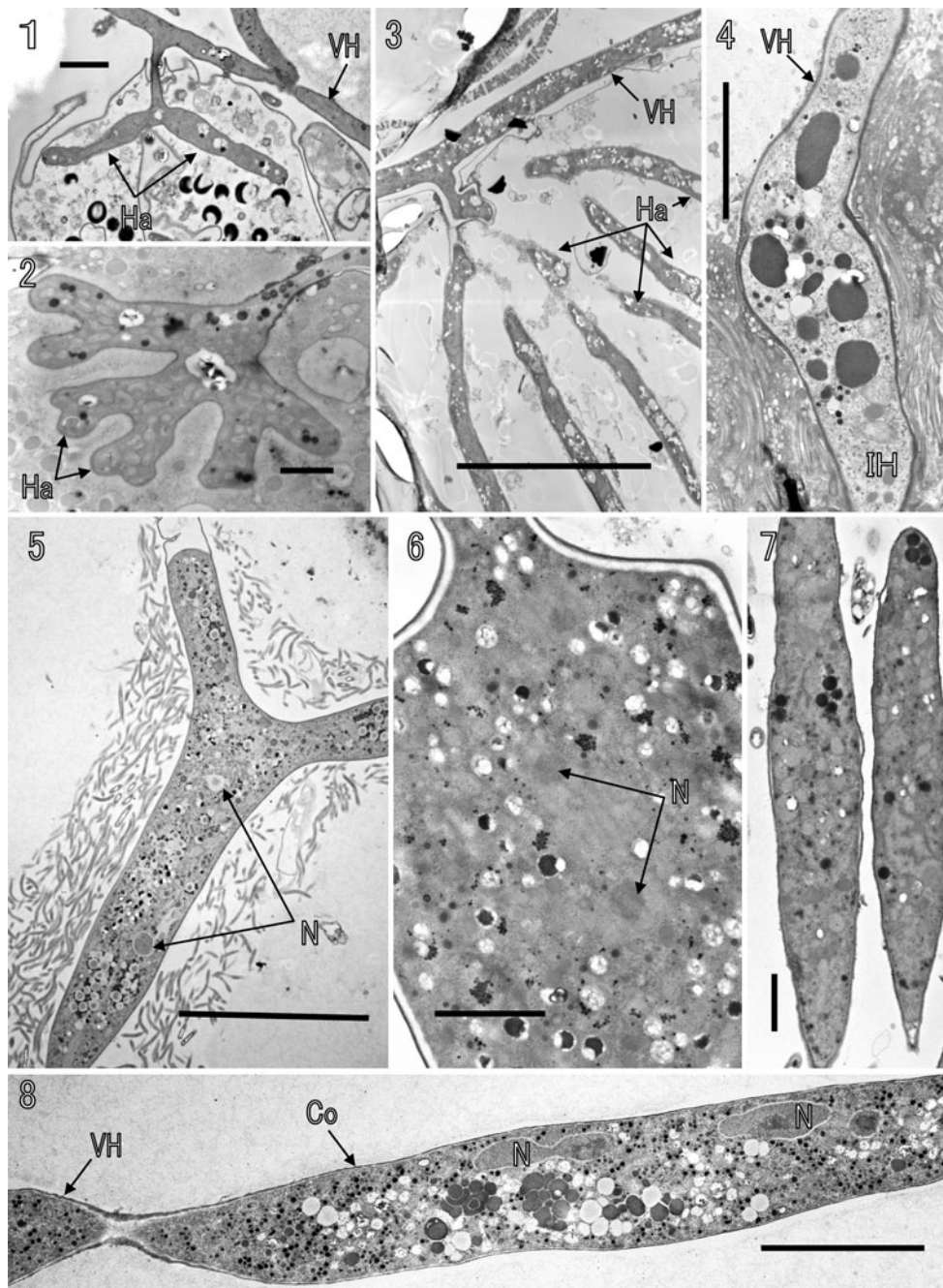
Zoopagaceae

Haustoria and infection hyphae

After capturing animals by adhesion, the vegetative hyphae of fungi in the Zoopagaceae develop haustoria or infection hyphae into the host animals to absorb nutrients. Testaceous- and non-testaceous rhizopods are known as hosts as well as nematodes, rotifers, and a species of the phylum Gastrotricha (Sommerstorff 1911). The shape and size of haustoria and infection hyphae depend strictly on the fungus species, e.g., the lobes of the haustorium in *Ac. rhabidospora* are short and thin (Fig. 1), those of *S. cephalote* are short but thick (Fig. 2), those of *Ac. tetraceros* are long and thin (Fig. 3), and those of *Zph. insidians* infecting rotifers grow throughout the entire body of a rotifer and, in the latter case, are no longer called haustoria but rather infection hyphae (Fig. 4). After absorption of nutrients, the protoplasm of the fungal structures in animals is also absorbed by vegetative hyphae leaving the cell walls. The absorption structures in ultrathin sections are, however, similar in morphology to each other; i.e., their coenocytic cell contains numerous electron-dense, and less dense, vesicles, 0.5–1.0 μm in diameter, in addition to ordinary cell organelles, such as nuclei and mitochondria, as shown in *S. rhabdospora* Drechsler (Saikawa 1986). Such vesicles were also shown in *Zph. pectosporus* (Saikawa and Morikawa 1985; Morikawa et al. 1993) and *Zph. insidians* (Whisler and Travland 1974; Morikawa et al. 1993), although larger vesicles (3.0–5.0 μm) were also seen in the portion of penetration of the infective hypha (Fig. 4).

Conidia

Asexual spores of fungi in the Zoopagaceae, together with those in the Cochlonemataceae, are conidia, although they are sometimes considered to be segments of merosporangium (Benjamin 1979; Cole and Samson 1979). Ultrathin sections of any spores in this family did not show the existence of cell walls of sporangium outside the cell walls of the spore proper in *Ac. dichotoma* (Fig. 5), *Ac. tetraceros* (Fig. 6), *S. cephalote* (Fig. 7), and *Zph. tentaculum* (Fig. 8), in contrast to the other taxa of Zygomycota (Beckett et al. 1974, figs. 140, 141). As shown by Saikawa (1986, fig. 10), the conidium often contained plural



Figs. 1–8 Electron micrographs of haustoria, infection hypha, and conidia in the Zoopagaceae. **1** A haustorium (*Ha*) of *Acaulopage raphidospora*. *VH*, vegetative hypha. **2** A haustorium (*Ha*) of *Stylopage cephalote*. **3** A haustorium (*Ha*) of *Ac. tetracosus*. *VH*, vegetative hypha. **4** An infection hypha (*IH*) of *Zoopagus insidians*.

VH, vegetative hypha. **5** A conidium of *Ac. dichotoma*. *N*, nucleus. **6** Central portion of conidium of *Ac. tetracosus*. *N*, nucleus. **7** Two conidia of *S. cephalote*. **8** A conidium (*Co*) of *Zph. tentaculum* before its liberation from a vegetative hypha (*VH*). *N*, nucleus. Bars **1, 2, 6, 7** 2 μ m; **3–5, 8** 10 μ m

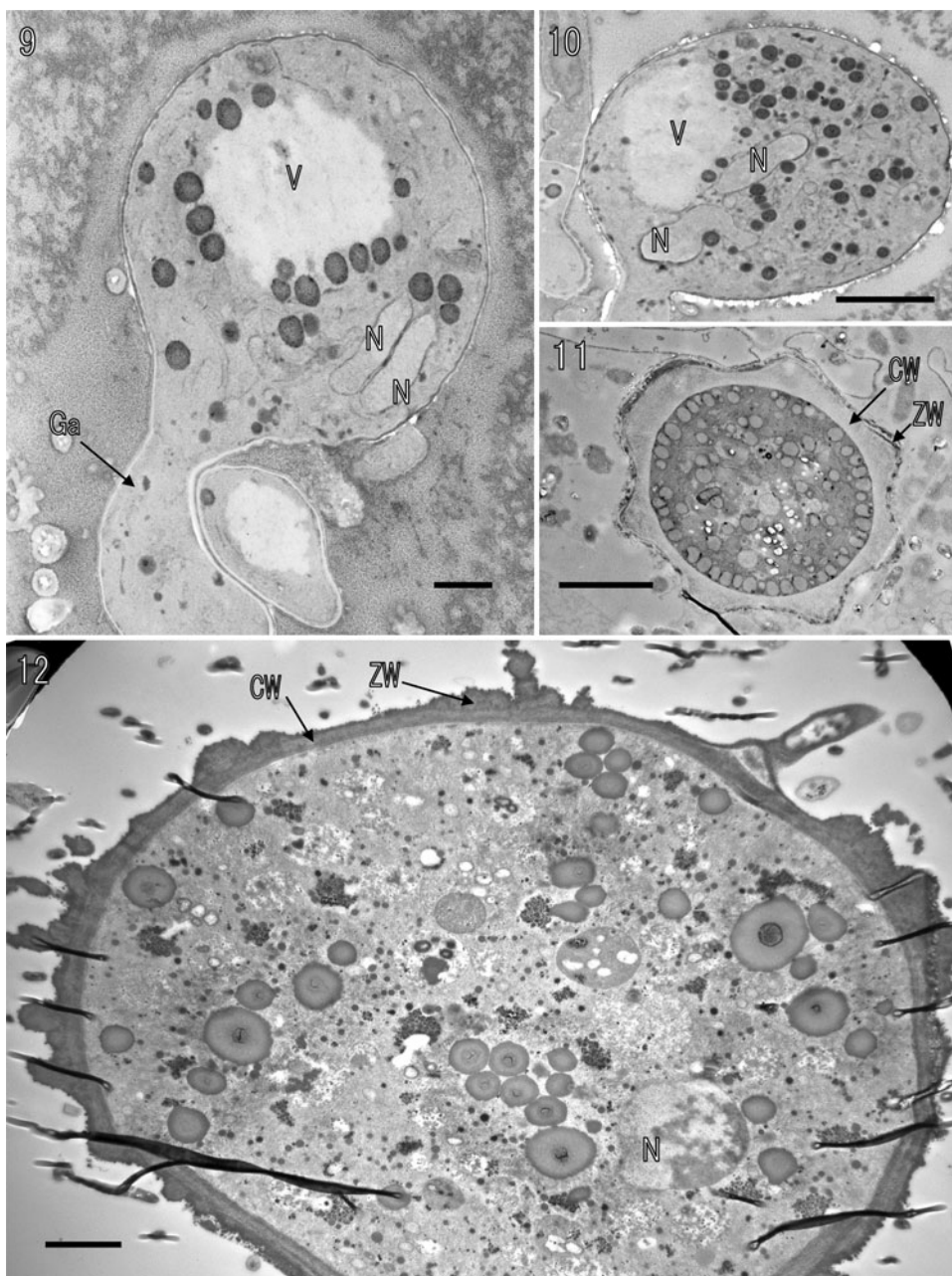
numbers of nuclei; often no nucleus, however, was observed in a thin section (Fig. 7).

Zygosporoes

After fusion by two gametangia, a globose zygosporangium emerges near the fusion point of the gametangia. In *Ac.*

raphidospora, paired nuclei were found in immature zygosporangia (Figs. 9, 10) that were in a developmental stage before their delimitation from the portion of respective suspensors by septa. The thick cell wall of the zygosporangium proper (Figs. 11, 12) appeared beneath the zygosporangial wall during maturation of a zygosporangium, in which the term “zygosporangium” is used for the combination of zygosporangium

Figs. 9–12 Electron micrographs of zygospores in the Zoopagaceae.
9, 10 Immature zygosporangia of *Acaulopage raphidospora*, each containing two nuclei (N). Ga, gametangium; V, vacuole.
11 A zygospore of *Ac. raphidospora*. The thick cell wall (CW) of the zygospore proper is covered entirely with the thin, electron-dense cell wall of the zygosporangium (ZW).
12 A zygospore of *Zoopagus pectosporus*. CW, cell wall; N, nucleus; ZW, zygosporangium cell wall.
 Bars 9–12 2 μ m



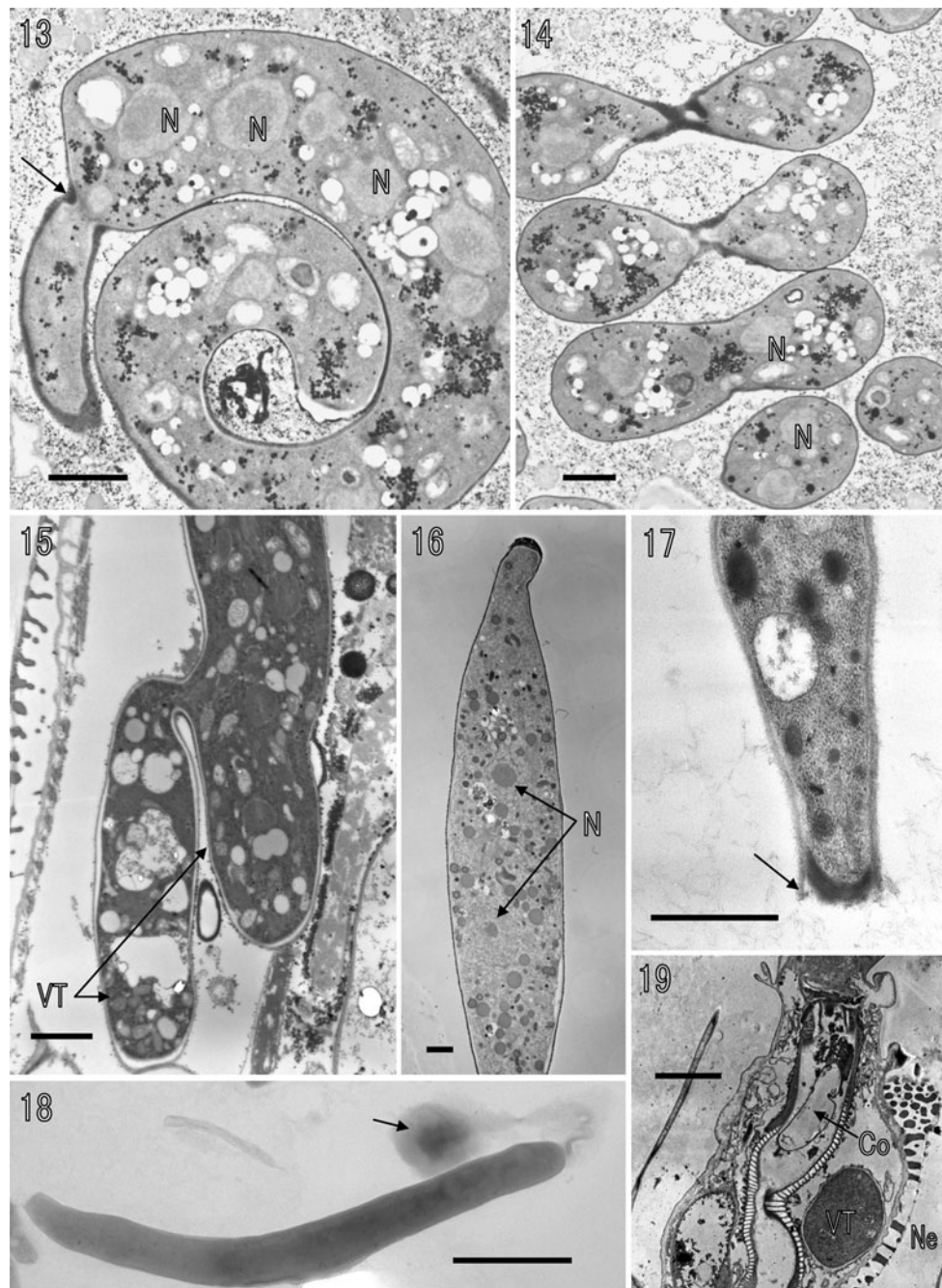
proper and zygosporangium (Benjamin 1959). More than one nucleus had never been observed previously in zygospores after maturation (Figs. 11, 12). The germination of zygospores has not yet been shown in electron micrographs, although Hirofani-Akabane and Saikawa (2010) observed it in *Ac. lophospora* Drechsler using an optical microscope.

Cochlonemataceae

Vegetative thalli

The vegetative hypha in the Zoopagaceae corresponds morphologically to the vegetative thallus in the

Cochlonemataceae growing in the host animals. The haustoria to absorb nutrients are not produced by fungi in this family except for *Amoebophilus* spp. (Dangeard 1910; Miura 1978; Barron 1983) and *B. helicoides* (Drechsler 1935a). Except that each species in *Euryancale* parasitizes nematodes, species in the Cochlonemataceae parasitize testaceous or non-testaceous rhizopods. In contrast to the Zoopagaceae, conidia can germinate only when they are in contact with the cuticle or pellicle of host, or are ingested by nematodes in *Euryancale*. The germination tube disappears when a young thallus is liberated from the distal end of the germination tube, although in at least eight species of *Cochlonema*, the germination tube persists

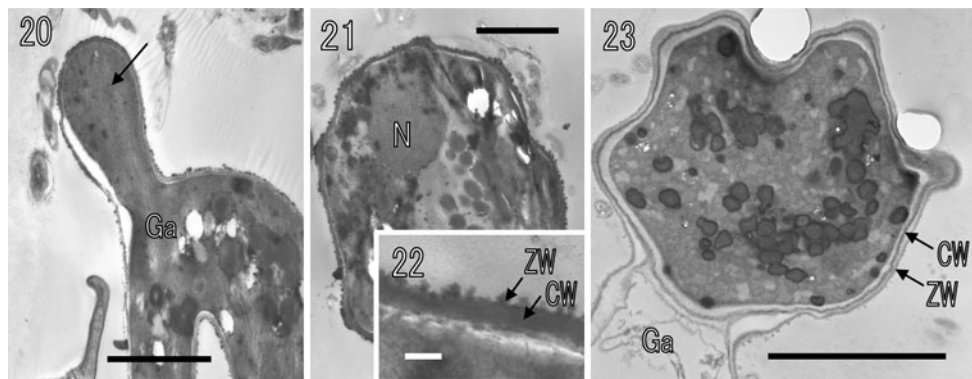


Figs. 13–19 Electron micrographs of vegetative thalli, conidia, and zygospores in the Cochlonemataceae. **13** A part of a coiled thallus of *Endocochlus gigas* in a rhizopod. *Arrow* shows the portion of dichotomous branching, although one of the two branches is outside this section. *N*, nucleus. **14** A peripheral part of a coiled thallus of *En. gigas* in a rhizopod. *N*, nucleus. **15** A part of vegetative thalli (*VT*) of *Euryancale marsipoides* in a nematode. **16** A conidium of *En. gigas*.

N, nucleus. **17** Basal end of conidium of *Cochlonema odontosperma*, showing the scar of disarticulation (*arrow*). **18** High-voltage electron micrograph of a conidium of *Eur. saccispora* in a 5- μ m-thick section. A pouchy appendage (*arrow*) is seen at its apical end. **19** A portion of a conidium (*Co*) of *Eur. marsipoides* in the esophageal lumen of a nematode. *N*, nucleus; *VT*, vegetative thallus. *Bars 13–19* 2 μ m

between conidium and thallus during the thallus development: the eight species are *Co. agamum* Drechsler (Drechsler 1946), *Co. cylindricum* Drechsler (Drechsler 1937), *Co. dolichosporum* Drechsler (Drechsler 1935a), *Co. euryblastum* Drechsler (Drechsler 1942), *Co. pigmaea*

Jones (Jones 1959), *Co. pumilum* Drechsler (Drechsler 1939b), *Co. symplocum* Drechsler (Drechsler 1941), and *Co. verrucosum* Drechsler (Drechsler 1935a). In most species of *Cochlonema* and *Endocochlus*, the young thallus grows into a coiled structure accompanied by dichotomous



Figs. 20–23 Electron micrographs of zygospores in the Cochlone-mataceae. **20** The bud of the zygosporangium (arrow) of *Cochlone-ma* (*Co.*) *odontosperma* developed from one of two gametangia (*Ga*) after fusion. **21** A zygospore of *Co. odontosperma*. *N*, nucleus. **22** Photographic enlargement of a part of **21**, showing cell walls of a

zygosporangium (*ZW*) and zygospore proper (*CW*). **23** A zygospore of *Euryancale marsipoides*. *CW*, cell wall of zygospore proper; *ZW*, zygosporangium cell wall; *Ga*, gametangium. Bars **20**, **21**, **23** 5 μ m; **22** 1 μ m

branching. The times of coiling and dichotomous branching depend on the species; for example, many such occurred in *En. gigas* (Figs. 13, 14), but only one time of coiling and no dichotomous branching were observed in *Co. cerasphorum* Drechsler (Hirotani-Akabane and Saikawa 2010). However, the vegetative thallus does not coil at all in most species of *Cochlone-ma* parasitizing various species of testaceous rhizopods (Drechsler 1937, 1939a,b, 1942, 1945, 1955) and in *Euryancale* spp. parasitizing nematodes (Fig. 15).

Conidia

As those in the Zoopagaceae, ultrathin sections of asexual spores of fungi in the Cochlone-mataceae exhibit the characteristics of conidia. On the cell wall of the conidium there were no additional walls *En. gigas* (Fig. 16) and in *Co. odontosperma* (Fig. 17) in the present study. The basal portion of conidia in *Co. odontosperma* after disarticulation (Fig. 17) was quite similar in general appearance of ultrastructure to that portion of anamorphic fungi (Cole and Samson 1979, figs. 4.35, 4.72, 4.73, 7.10). The conidium often contained plural numbers of nuclei (Fig. 16), as shown in *Co. odontosperma* (Saikawa and Sato 1991, fig. 10). In the present study a conidium of *Eur. marsipoides* was found in the esophageal lumen of a nematode in the genus *Bunonema*, although it was already empty of protoplasm (Fig. 19). As shown in *Eur. phallospora* Saikawa & Katsurashima (Saikawa and Katsurashima 1993), infection of nematodes by *Euryancale* spp. would be initiated by conidia that were swallowed by the animals such as those in sickle- or helical-shaped conidia in *Harposporium* spp. (Aschner and Kohn 1958; Saikawa et al. 1983; Saikawa and Endo 1986). As does that of

Harposporium spp., *Euryancale* spp. also has a pouchy appendage at one end of the conidium (Fig. 18).

Zygospores

The zygothoric hyphae develop on two compatible thalli. Similar to that in the Zoopagaceae, each of the zygothoric hyphae produces a septum to delimit the gametangium before fusion. The gametangium becomes thickened gradually and more or less twists with another gametangium. After fusion, however, the zygosporangium develops from one of the gametangia as a bud in the Cochlone-mataceae (Fig. 20). The thick cell wall of the zygospore proper appeared beneath the zygosporangial cell wall. The thickness of the walls after maturation of zygospores in *Co. odontosperma* (Figs. 21, 22) and *Eur. marsipoides* (Fig. 23) was somewhat thinner than that in the Zoopagaceae (Figs. 11, 12). Although germination of zygospores in *Co. cerasphorum* and *Co. megalosomum* Drechsler was shown by Hirotani-Akabane and Saikawa (2010) using optical techniques, no ultrastructural study has yet been done.

Conclusions

Since Drechsler (1935a, b, c) described 10 species of Zoopagaceae and 4 species of Cochlone-mataceae in 1935, 66 species and five varieties in the former family and 33 species and one variety in the latter have been described (Saikawa 2010). The numbers of species and varieties are not small, but a recently published textbook of mycology (Webster and Weber 2007) omitted the two families from the article of the order Zoopagales (sensu Benjamin 1979),

and a recent phylogenetic scheme by Tanabe et al. (2004) did not include the two families from the clade of the Zoopagales, but *Piptocephalis freseniana* de Bary, *Kuzuhaea moniliformis* R.K.Benj., and *Syncephalis depressa* Tiegh. & G. Le Monn. were included. These three species were once members of the order Mucorales producing the merosporangium (Benjamin 1959). In a review on Zygomycetes (Benny et al. 2001), ultrastructural evidence of asexual spores of *S. rhabdospora* (Saikawa 1986) was the only article in the section for the two families. Thus, aspects on ultrastructure of conidia and zygospores were added to the current poor information on the Zoopagaceae and Cochlonemataceae in this review.

Acknowledgments I thank Drs. Koichiro Miura, Sakado, Saitama, Japan and Seiji Tokumasu, Ueda, Nagano, Japan, very much for introducing me to mycology when they were, respectively, an associate professor and a graduate student, Tokyo Kyoiku University (currently, University of Tsukuba), Bunkyo-ku, Tokyo, Japan, about 40 years ago. I also thank Drs. Hiroki Sato, Kyushu Research Center, Forestry and Forest Products Research Institute, Kumamoto, Kumamoto, Japan, and Chiharu Morikawa, Ishikawa Agriculture Center, Kanazawa, Ishikawa, Japan, for their nomination of me as a candidate for the award of the Mycological Society of Japan 2008 and also for their encouragement during the study. I am also grateful to my students Mr. Yuji Aoki, Mr. Masao Goho, Mr. Toru Kadowaki, Mr. Hajime Makii, Ms. Yuki Masumura, and Ms. Yuka Wakai, Tokyo Gakugei University, Koganei, Tokyo, Japan, for their help, mainly in collecting and culturing zygomycotan fungi used in the present study. I am indebted to Dr. Tatsuo Arai, National Institute for Physiological Sciences, Okazaki, Aichi, Japan, for his help in operating the high-voltage electron microscope.

References

- Aschner M, Kohn S (1958) The biology of *Harposporium anguillulae*. J Gen Microbiol 19:182–189
- Barron GL (1983) A new *Amoebophilus* (Zygomycetes) ectoparasitic on amoebae. Can J Bot 61:3091–3094
- Beckett A, Heath IB, McLaughlin DJ (1974) An atlas of fungal ultrastructure. Longman, London
- Benjamin RK (1959) The merosporangiferous Mucorales. Aliso 4:321–433
- Benjamin RK (1979) Zygomycetes and their spores. In: Kendrick B (ed) The whole fungus: the sexual–asexual synthesis, vol 2. National Museums of Canada, Ottawa, pp 573–616
- Benny GL, Humber RA, Morton JB (2001) Zygomycota: Zygomycetes. In: McLaughlin DJ, McLaughlin EG, Lemke PA (eds) The Mycota, vol VII(A). Systematics and evolution. Springer, Berlin, pp 113–146
- Ciccarone C (1989) *Acaulopage tigrina* sp. nov. e *Drepanoconis divertigastra* sp. nov.: due componenti nuovi di generi microfungi poco noti. Micol Ital 18:29–32
- Cole GT, Samson RA (1979) Patterns of development in conidial fungi. Pitman, London
- Dangeard PA (1910) Études sur le développement et la structure des organismes inférieurs. I. Les Amibes. Le Botaniste 11:4–57
- Drechsler C (1933) Morphological features of some fungi capturing and killing amoebae. J Wash Acad Sci 23:200–202
- Drechsler C (1935a) Some conidial phycomycetes destructive to terricolous amoebae. Mycologia 27:6–40
- Drechsler C (1935b) Some non-catenulate conidial phycomycetes preying on terricolous amoebae. Mycologia 27:176–205
- Drechsler C (1935c) A new species of conidial phycomycete preying on nematodes. Mycologia 27:206–215
- Drechsler C (1936) New conidial phycomycetes destructive to terricolous amoebae. Mycologia 28:363–389
- Drechsler C (1937) New Zoopagaceae destructive to soil rhizopods. Mycologia 29:229–246
- Drechsler C (1939a) A few new zoopagaceae destructive to large soil rhizopods. Mycologia 31:128–153
- Drechsler C (1939b) Five new zoopagaceae destructive to rhizopods and nematodes. Mycologia 31:388–415
- Drechsler C (1941) Four phycomycetes destructive to nematodes and rhizopods. Mycologia 33:248–269
- Drechsler C (1942) New species of *Acaulopage* and *Cochlonema* destructive to soil amoebae. Mycologia 34:274–297
- Drechsler C (1945) Several additional phycomycetes subsisting on nematodes and amoebae. Mycologia 37:1–31
- Drechsler C (1946) Three new zoopagaceae subsisting on soil amoebae. Mycologia 38:120–143
- Drechsler C (1947) Three zoopagaceous fungi that capture and consume soil-inhabiting rhizopods. Mycologia 39:253–281
- Drechsler C (1955) Additional species of Zoopagaceae subsisting on rhizopods and eelworms. Mycologia 47:364–388
- Hibbett DS, Binder M, Bischoff JF, Blackwell M, Cannon PF, Eriksson OE, Huhndorf S, James T, Kirk PM, Lücking R, Lumbsch HT, Lutzoni F, Matheny PB, McLaughlin DJ, Powell MJ, Redhead S, Schoch CL, Spatafora JW, Stalpers JA, Vilgalys R, Aime MC, Aptroot A, Bauer R, Begerow D, Benny GL, Castlebury LA, Crous PW, Dai YC, Gams W, Geiser DM, Griffith GW, Gueldan C, Hawksworth DL, Hestmark G, Hosaka K, Humber RA, Hyde KD, Ironside JE, Kõljalg U, Kurtzman CP, Larsson KH, Lichtwardt R, Longcore J, Miadlikowska J, Miller A, Moncalvo JM, Mozley-Standridge S, Oberwinkler F, Parmasto E, Reeb V, Rogers JD, Roux C, Ryvarden L, Sampaio JP, Schüßler A, Sugiyama J, Thorn RG, Tibell L, Untereiner WA, Walker C, Wang Z, Weir A, Weiß M, White MM, Winka K, Yao YJ, Zhang N (2007) A higher-level phylogenetic classification of the Fungi. Mycol Res 111:509–547
- Hirotsani-Akabane E, Saikawa M (2010) Germination and morphology of zygospores in two *Cochlonema* and one *Acaulopage* species. Mycologia 102:39–43
- Jones FR (1959) Some Zoopagales from Kenya. Trans Brit Mycol Soc 42:75–89
- Jones FR (1962) New English Zoopagales. Trans Brit Mycol Soc 45:348–358
- Kirk PM, Cannon PF, David JC, Minter DW, Stalpers JA (2008) Ainsworth and Bisby's dictionary of the fungi, 10th edn. CAB International, Oxon
- Miura K (1978) *Amoebophilus dangeardii*, a new zygomycete parasitic on amoebae. J Jpn Bot 53:184–192
- Morikawa C, Saikawa M, Barron GL (1993) Fungal predators of rotifers: a comparative study of *Zoopagus*, *Lecophagus* and *Cephalophora*. Mycol Res 97:421–428
- Saikawa M (1986) Ultrastructure of *Stylopaga rhabdospora*, an amoeba-capturing Zoopagaceous fungus. Mycologia 78:309–312
- Saikawa M (2010) On fungi in the Zoopagaceae and Cochlonemataceae. Nippon Kingakukai Kaiho (in Japanese, in review)
- Saikawa M, Endo J (1986) An electron microscope study of the infection of nematodes by conidia of *Harposporium diceraeum*. Trans Mycol Soc Jpn 27:341–347
- Saikawa M, Kadowaki T (2002) Studies on *Acaulopage dichotoma* and *A. tetracerus* (Zoopagales, Zygomycota) capturing amoebae. Nova Hedwigia 74:365–371
- Saikawa M, Katsurashima E (1993) Light and electron microscopy of a new species of *Euryancale* producing phallus-shaped conidia. Mycologia 85:24–29

- Saikawa M, Morikawa C (1985) Electron microscopy on a nematode-trapping fungus, *Acaulopage pectospora*. *Can J Bot* 63: 1386–1390
- Saikawa M, Sato H (1991) Ultrastructure of *Cochlonema odontosperma*, an endoparasite in amoebae. *Mycologia* 83:403–408
- Saikawa M, Totsuka J, Morikawa C (1983) An electron microscope study of initiation of infection by conidia of *Harposporium oxycoracum*, an endozoic nematophagous hyphomycete. *Can J Bot* 61:893–898
- Sommerstorff H (1911) Ein Tiere fangender Pilz. (*Zoophagus insidians*, nov. gen., nov. spec.). *Österreichische Botanische Zeitschrift* 61:361–373
- Tanabe Y, Saikawa M, Watanabe MM, Sugiyama J (2004) Molecular phylogeny of Zygomycota based on EF-1 α and RPB1 sequences: limitations and utility of alternative markers to rDNA. *Mol Phylogenet Evol* 30:438–449
- Webster J, Weber RWS (2007) *Introduction to fungi*, 3rd edn. Cambridge University Press, Cambridge
- Whisler HC, Travland LB (1974) The rotifer trap of *Zoophagus*. *Arch Microbiol* 101:95–107