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A new *Halophytophthora* species, *H. porrigovesica*, from subtropical and tropical mangroves

Akira Nakagiri[1)]*, Tadayoshi Ito[1)], Leka Manoch[2)] and Morakot Tanticharoen[3)]

[1)] Institute for Fermentation, Osaka (IFO), 17–85, Juso-honmachi 2-chome, Yodogawa-ku, Osaka 532–8686, Japan
[2)] Kasetsart University, Chatuchak, Bangkok 10900, Thailand
[3)] National Center for Genetic Engineering and Biotechnology (BIOTEC), 73/1 Rama VI Rd., Bangkok 10400, Thailand

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A new oomycete was found from intertidal fallen leaves of mangroves in Japan and Thailand and is described here as *Halophytophthora porrigovesica*. This species is characterized by having an epapillate, ovate zoosporangium with a lens-shaped dehiscence plug-like material at the apex, and by forming an expanding long cylindrical vesicle prior to zoospore release. A key to 14 species and 2 varieties of *Halophytophthora* including the new species is proposed. The subtropical (Iriomote Is., Japan) strains and tropical (Thailand) strains were different in physiological properties and especially in the asexual reproduction. The subtropical strains showed a lower optimal temperature and wider range of suitable temperature and salinity for zoosporangium formation, whereas the tropical strains showed a higher optimal temperature and narrower range of temperature and salinity. These differences are explained as adaptations of the strains to the environmental conditions of their respective habitats. From the subtropical mangroves, six strains of the new species have been isolated only from submerged leaves of *Sonneratia alba*, while several strains have been isolated from tropical mangroves from the leaves of three species of mangrove trees, *S. alba, Bruguiera gymnorrhiza* and *Avicennia alba*. This indicates a change of taxon selectivity (host specificity) with the geographical distribution.

Key Words——geographical distribution; *Halophytophthora porrigovesica*; mangrove; taxon selectivity.

Since the first description of *Halophytophthora vesicula* (Anastasiou & Churchl.) H. H. Ho & S. C. Jong as *Phytophthora vesicula* Anastasiou & Churchl. (1969), 13 species and 2 varieties of *Halophytophthora* H. H. Ho & S. C. Jong have been described from marine and brackish water environments, especially from mangroves in subtropical and tropical regions (Fell and Master, 1975; Pegg and Alcorn, 1982; Gerettson-Cornell and Simpson, 1984; Ho et al., 1991, 1992; Nakagiri et al., 1994). Ecological studies revealed halophytophthoras are the first colonizers on submerged mangrove leaves after leaf fall (Newell et al., 1987; Nakagiri et al., 1989). Their growth and reproduction behaviors were found to be well adapted to the intertidal brackish water of mangroves, where salinity and temperature of the water fluctuate greatly with daily tidal rhythms (Nakagiri, 1993). Geographical and seasonal distributions of halophytophthoras were observed in subtropical mangroves (Nakagiri, 1993; Nakagiri et al., 1996). Species dominance along a river with different water salinities and occurrence of species at different seasons was also investigated (Nakagiri, 2000). These ecological studies revealed that each species of *Halophytophthora* has its own physiological properties and occurs where and when the environmental factors, such as salinity and temperature, are suitable, and that some species have a preference for leaves of a specific mangrove tree.

In the course of comparative studies of the diversity of halophytophthoras in subtropical (Japan) and tropical (Thailand) mangroves, an undescribed species of *Halophytophthora* was discovered. This species had been isolated repeatedly from submerged fallen leaves of *Sonneratia alba* J. E. Sm. on Iriomote Is. (Okinawa, Japan), but not from other mangrove trees. Meanwhile, the same species was discovered from Thai mangroves. In Thai mangroves, several strains were isolated from fallen leaves of three kinds of mangrove trees including *S. alba*. This species has unique characteristics in its epapillate zoosporangium and extending vesicle at the opening of the zoosporangium. Thus, we describe here the new species of *Halophytophthora* and give a key to all the known species of the genus *Halophytophthora*. Because the new species was found to inhabit different environments, we compared the isolates from the subtropical and the tropical mangroves in their growth and reproductive properties to investigate their ecological diversities that may correspond to the geographical distribution.

Materials and Methods

Isolation Submerged fallen leaves of mangrove trees, *Avicennia marina* (Forsk.) Vierh., *Bruguiera gymnorrhiza* Lamk., *Kandelia candel* Druce, *Rhizophora stylosa* Griff.

*Corresponding author. E-mail: nakagiri-akira@ifo.or.jp

and *Sonneratia alba*, were collected at river mouth of the Shiira River, Iriomote Is., Okinawa, Japan in cool (Nov.-Feb.; air temp., 15–22°C) and warm (Jul.-Sept.; 25–31°C) seasons from 1997 to 1998. Halophytophthoras were isolated by removing disks from leaf samples and plating washed and drained disks on cornmeal seawater agar (CMSWA: cornmeal agar (Nissui, Tokyo) dissolved in 20 ppt salinity seawater (Jamarin S; Jamarin Lab., Osaka). From the leaf samples, *H. vesicula* and *H. spinosa* var. *lobata* (Fell & Master) H. H. Ho & S. C. Jong dominantly appeared especially in the warm season, but *H. exoprolifera* H. H. Ho, Nakagiri & S. Y. Newell and *H. avicenniae* (Gerr.-Corn. & J. A. Simpson) H. H. Ho & S. C. Jong were less frequent. Six strains of the new species were isolated only from fallen leaves of *S. alba,* collected in Jul. 1997 and Feb. and Sep. 1998. In Mar. 1999, we investigated halophytophthoras from submerged fallen leaves of eight species of mangrove trees at Ranong and Phang-nga in Thailand. Three strains of the new species were isolated from submerged leaves of *B. gymnorrhiza*, *Avicennia alba* Bl. and *S. alba*. Two strains each of the subtropical (Japan) and the tropical (Thailand) isolates, AN-1587 (=IFO 33159), AN-1588 (=IFO 33160) and MT-88 (=BCC 6573=IFO 33161), MT-95 (=BCC 6579=IFO 33162), were employed for observation of morphology and comparison of their growth and reproductive properties.

Observation Isolates were cultured and observed on vegetable juice seawater agar (VJSWA-20) (Nakagiri et al., 1994). Zoosporangia formation and zoospore release were induced by submerging agar disks with mycelia in 20 or 30 ppt salinity seawater. Scanning electron microscopy (SEM) was also performed to observe fine structures and the development process of zoosporangia and vesicles after fixing the material with 1% OsO_4 in 10 ppt seawater.

Culture tests Growth and asexual reproduction of the above four strains were examined at different salinities and temperatures in the manner described previously (Nakagiri, 1993), to compare properties of the subtropical and tropical isolates.

Results

Taxonomy

Halophytophthora porrigovesica Nakagiri, Tad. Ito, Manoch & Tanticharoen, sp. nov. Figs. 1–29

Coloniae in VJSWA-20 seleriter crescentes, obscure rosulatae, ad 20–25°C 5–7 mm per diem extendentes, mycelio aerio lanoso exigue obductae. Hyphae ramosae, 3–8 μm diam, aseptatae. Zoosporangiophora usque ad 1400 μm longa, 2–6 μm diam, irregulariter vel sympodialiter ramosa. Zoosporangia hyalina vel subhyalina, laevia, ovata vel obovata, epapillata, persistentia, (32–) 72–88 (–125) × (22–) 44–69 (–82) μm, ad apicem materiam hyalinam lentiformem obturamentaceam (20–30 μm diam, medio 4–12 μm crassa) cumulata. Ante liberationem zoosporae ex apice sporangii vesicula leptoderma cylindracea uspue ad 320 μm longa 10–20 μm lata enata. Zoosporae per foramen in apice vesiculae elabens, subglobosae vel ovatae, 8–10 × 10–14 μm, a latere biflagellatae, post incystem tubis germinationis 1–2 pullulantes. Oogonia non visa.

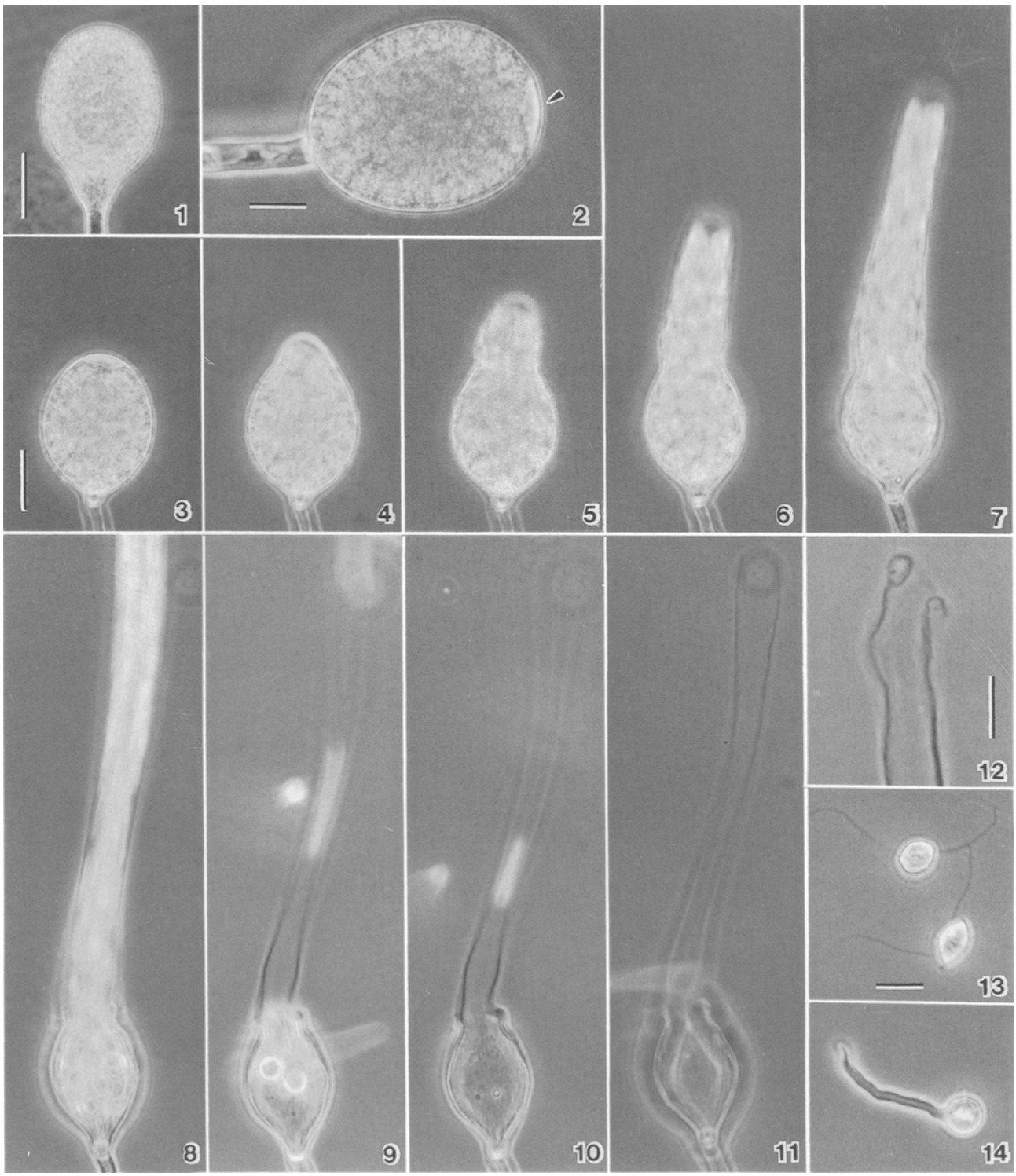
Holotypus: IFO H-12232, specimen in lamina vitrea ex cultura AN-1587 (IFO 33159) ex fronde dejecta submersaque *Sonneratiae albae* J. E. Sm., Shiira Riv., Iriomote Is., Okinawa, Japonia, July 1997, a A. Nakagiri isolatum, in Herbario IFO conservatum.

Etymology: From the Latin *porrigens*=expanded, *vesica*=bladder, referring to the expanding and long vesicle.

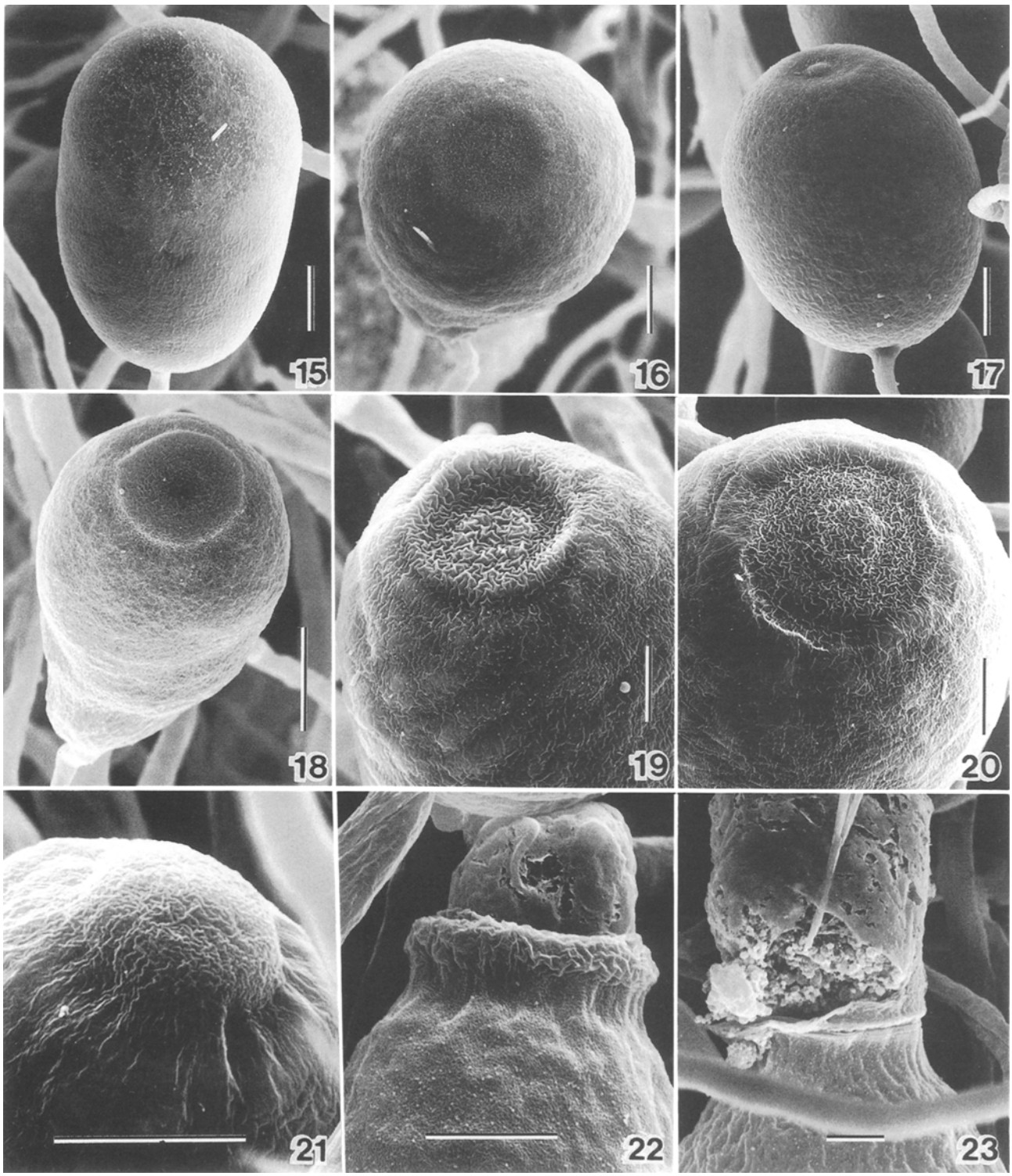
Colonies on VJSWA-20 faintly rosette with scanty lanose aerial mycelium. Growth is rapid (5–7 mm/d on VJSWA-20 at 20–25°C). Hyphae branched, smooth, 3–8 μm in diam, non-septate. Zoosporangiophores often indistinct from vegetative hyphae, up to 1400 μm long, 2–6 μm in diam. Branching irregularly or sometimes sympodially (without apparent pattern). Zoosporangia formation occurs on the surface of VJSWA-20, though enhanced by submersion in seawater. Zoosporangium is separated from the zoosporangiophore by 2–4 μm thick plug (or septum) below the sporangium, which develops with maturation of the zoosporangium. Zoosporangia hyaline to subhyaline, smooth, ovate to obovate, without papilla, non-deciduous, (32–) 72–88 (–125) × (22–) 44–69 (–82) μm ($\bar{x}$ = 76 × 55 μm), length/breadth ratio (0.85–) 1.11–1.47 (–2.42). With the maturation (zoospore differentiation), a transparent lens-shaped plug-like material (20–30 μm in diam, 4–12 μm thick at the middle) deposits at the apex of the zoosporangium (Fig. 2). Wall of the apex of zoosporangium is thin and lined with the plug-like material. Prior to zoospore release, the apex of the zoosporangium swells and elongates into a thin-walled vesicle (Figs. 3–7). Vesicle cylindrical, up to 320 μm long, 10–20 μm wide. At the apex of the elongating vesicle, the plug-like material is visible. When the vesicle is fully stretched, the apex tears to make an opening (Fig. 12), through which zoospores swim away (Figs. 3-11). After zoospore release, the vesicle shrinks in length and width, but does not retract completely as in the mangrove strains of *H. vesicula* (Nakagiri, 1993) and persists for a day or more. Zoospores subglobose to ovate, laterally biflagellate, 8–10 × 10–14 μm (Fig. 12). Encysted zoospores germinating via one or two hyphae (Fig. 14). Oogonia not formed alone or in combination with the strains isolated in this study.

Holotype: IFO H-12232, voucher slides of the strain AN-1587 (IFO 33159) isolated from submerged decaying leaf of *Sonneratia alba*, from the Shiira River, Iriomote Is., Okinawa, Japan, July 1997, deposited in the herbarium of the Institute for Fermentation, Osaka (IFO).

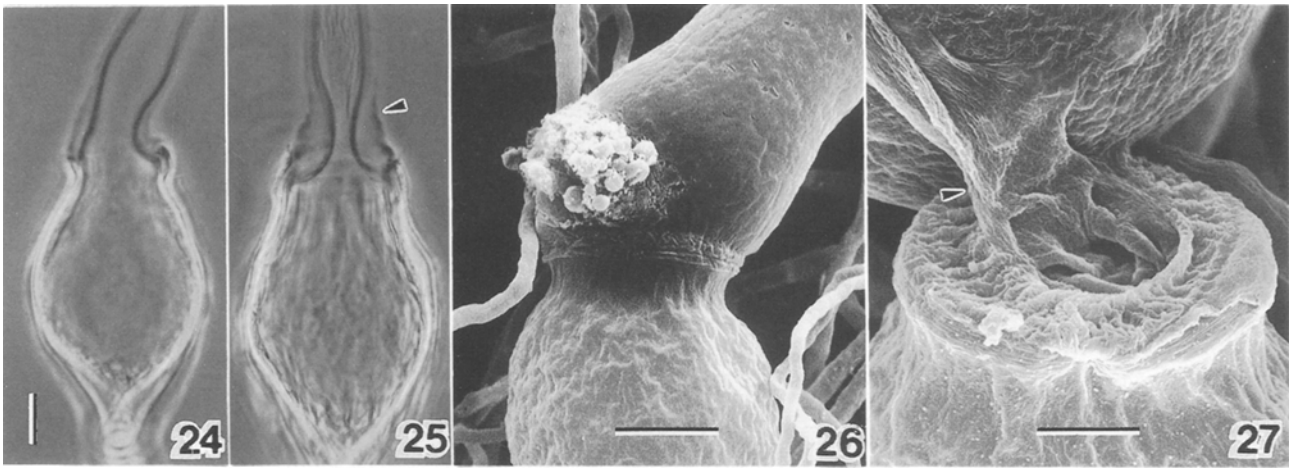
Other specimens examined: IFO H-12233 [voucher slides of the strain AN-1588 (IFO 33160) isolated from submerged decaying leaf of *S. alba*, from the Shiira River, July 1997]; IFO H-12234 and IFO H-12235 [voucher slides of the strains MT-88 (=BCC 6573=IFO 33161) and MT-95 (=BCC 6579=IFO 33162), isolated from submerged decaying leaf of *Bruguiera gymnorrhiza*, from



Figs. 1–14. Light micrographs of *H. porrigovesica*. 1. Young zoosporangium. 2. Mature zoosporangium, in which zoospores have differentiated. Note the lens-shaped, transparent plug-like material (arrowhead) deposited at the apex of zoosporangium. 3–11. Serial photos of vesicle formation and zoospore release. This process (from Fig. 4 to Fig. 8) was performed in a few seconds. 12. An opening at the apex of vesicle, through which zoospores swim away. 13. Biflagellate zoospores. 14. An encysted zoospore germinating a hypha. Bars: 1, 3 (=4–11)=20 μm; 2, 12, 13 (=14)=10 μm.



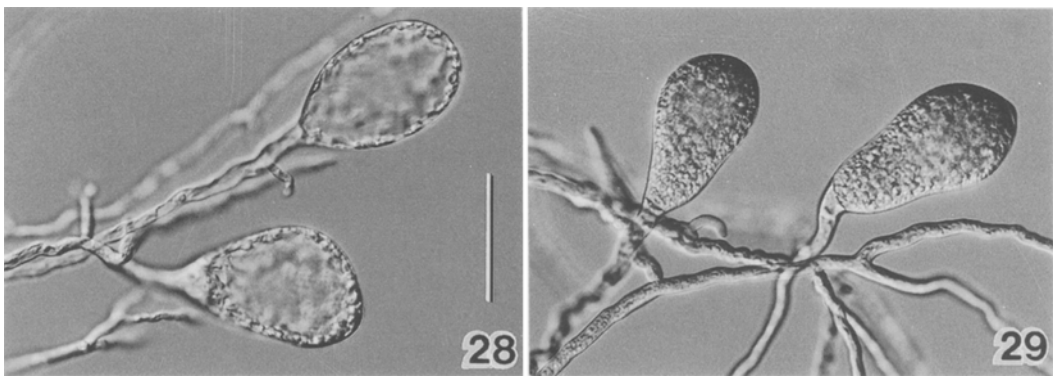
Figs. 15–23. Scanning electron micrographs of *H. porrigovesica*, showing the development process of zoosporangium and vesicle. 15. Young zoosporangium. 16. Disk-like feature at the apex of young zoosporangium, corresponding to the dehiscence plug-like material deposited beneath the apical wall. 17–19. Ring-shaped (or donut-shaped) plug-like materal of maturing zoosporangium. 20. Loose appearance of the apical wall of zoosporangium, especially at the place lined with the plug-like materal. 21. Center of the ring-shaped plug-like materal rising outward to form a vesicle. 22, 23. Extending vesicle through the opening at the apex of zoosporangium. Bars: 15–18=10 μm; 19–23=5 μm.



Figs. 24–27. Light and scanning electron micrographs of *H. porrigovesica*. 24. Vacant zoosporangium just after zoospore release, showing expanded vesicle. 25. Zoospore-discharged, old zoosporangium with wrinkled inner wall and shrunken vesicle. Note mucilaginous material (arrowhead) deposited around the opening of zoosporangium and along the vesicle membrane. 26. An expanded vesicle containing zoospores. 27. Constricted opening of zoospore-discharged zoosporangium. Note a vesicle membrane (arrowhead) remaining at the opening. Bars: 24 (=25), 26=10 μm; 27=5 μm.

Phang-nga mangrove, Thailand, March 1999 and from submerged decaying leaf of *Avicennia alba*, from Ranong mangrove, Thailand, March 1999, respectively].

The process of zoosporangium development and vesicle formation of *H. porrigovesica* is peculiar among *Halophytophthora* species. When zoospores began to differentiate within a zoosporangium, a lens-shaped plug-like material deposited at the apex of ovate or obovate zoosporangium (Figs. 1, 2, 15, 16). As the zoospore formation proceeded, the external appearance (under SEM) of the plug-like material became ring-shaped (or donut-shaped) (Figs. 17–19). At the maturation of the zoosporangium, the surface of the apical wall became loose (Fig. 20). Then, the membranaceous wall of the center of the ring began to rise outward (Fig. 21) and extend into a long vesicle (Figs. 22, 23). The origin of the vesicle membrane was not certain, but the plug-like material or a plasma membrane under the apex of the zoosporangium may be involved in the formation of the vesicle. The extension of the vesicle was complete within a few seconds (Figs. 3–11). Zoospores (Fig. 13) were liberated through the opening of the apex of the vesicle (Fig. 12). After zoospore release, the vesicle began to shrink both in length and width (Figs. 24–27). Zoospore-discharged sporangia often had a wrinkled inner wall and a shrunken vesicle that was constricted at the opening of the sporangium (Fig. 25). SEM showed the opening of the sporangium was constricted to a narrow path where a vesicle membrane remained after zoospore release (Fig. 27). At the proximal end of the vesicle, a mucilaginous material, which possibly derived from the plug-like material, was observed surrounding the opening of the sporangium and along the vesicle membrane (Fig. 25). All these characteristics of zoosporangium development, especially the vesicle formation, are unique among the *Halophytophthora* species described so far.



Figs. 28, 29. Light micrographs of *H. porrigovesica*, showing zoosporangia produced by subtropical and tropical strains submerged in 37°C seawater. 28. Aborted zoosporangia, whose protoplasm was lost, produced by the subtropical strain (AN-1587=IFO 33159). 29. Normal zoosporangia produced by the tropical strain (MT-88=BCC 6573=IFO 33161). Bar: 28 (=29)=50 μm.

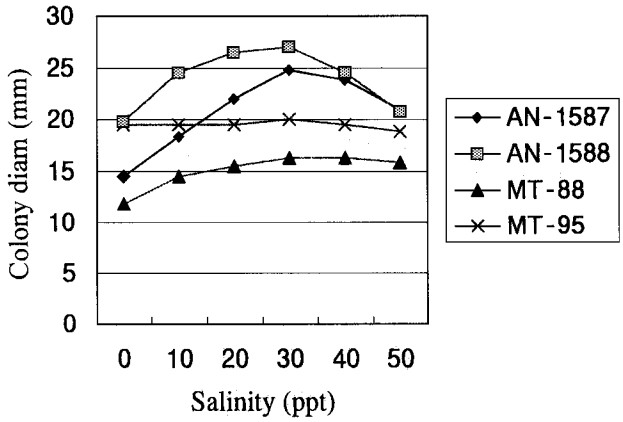


Fig. 30. Hyphal growth of *H. porrigovesica* strains after 4 d of incubation at 25°C on VJSWA with different salinities.

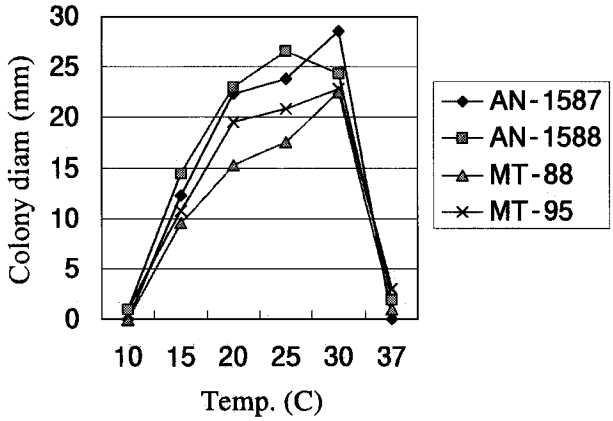


Fig. 31. Hyphal growth of *H. porrigovesica* strains after 4 d of incubation on VJSWA with 30 ppt salinity at different temperatures.

Comparison of subtropical and tropical isolates

Hyphal growth Both Iriomote (subtropical) and Thai (tropical) isolates of *H. porrigovesica* showed optimal growth on VJSWA with 30 ppt salinity when they were cultured at 25°C, though they could grow in a wide range of salinity from 0 to 50 ppt (Fig. 30), which may be evidence that this species adapts to mangrove brackish water environments. As for the temperature, the strains grew well in the range between 20 and 30°C on the 30 ppt salinity VJSWA plates. The subtropical isolates (AN-1887 and AN-1588) showed optimal growth at 25 or 30°C, while the tropical isolates (MT-88 and MT-95) at 30°C (Fig. 31). No remarkable difference was observed among the strains in the hyphal growth properties at different salinities and temperatures.

Asexual reproduction Zoosporangia formation was enhanced by submerging agar blocks with mycelia in seawater for a half or one day, in the same way as other species of *Halophytophthora*. Tests for salinity effects on zoosporangia formation showed that the optimum was 30 ppt for both subtropical and tropical strains, but the former strains were well reproductive over a wider range of salinity (10–50 ppt), whereas the latter showed preference for a narrower range (20–40 ppt) (Table 1). The temperature causing better zoosporangia formation was different between the subtropical and tropical strains. The subtropical strains were reproductive over a wider range of temperature from 15 to 30°C with the optimum at 25°C, whereas the tropical strains produced zoosporangia well at 25–37°C, most abundantly at 30°C (Table 2). Difference was also observed in the response to submersion in 37°C seawater. The subtropical strains could form zoosporangia in such high temperature seawater, but most of them were aborted by loosing protoplasm (Fig. 28), whereas the tropical strains mostly produced normal zoosporangia without abortion (Fig. 29). Thus, the tropical strains showed preference for and greater resistance to high temperature than the subtropical strains.

Discussion

A variety of zoosporangia morphology is observed in the genus *Halophytophthora*, e.g., smooth walled or ornamented, with or without papilla, dehiscence plug and vesicle. Among the previously known 13 species of *Halophytophthora*, epapillate zoosporangia are formed in three species, *H. avicenniae* (Gerr.-Corn. & J. A. Simpson) H. H. Ho & S. C. Jong, *H. kandeliae* H. H. Ho, H. S. Chang & S. Y. Hsieh and *H. operculata* (Pegg & Alcorn) H. H. Ho & S. C. Jong. The new species, *H. porrigovesi*

Table 1. Zoosporangium formation of *H. porrigovesica* induced by submersion in seawater of different salinities at 25°C.

	0	10	20	30	40	50(ppt)
AN-1587[2)]	+[1)]	++	+++	++++	++++	++
AN-1588	+	++	++++	++++	+++	++
MT-88	±	+	++	+++	++	+
MT-95	±	+	+++	+++	++	+

[1)] Relative abundance of produced zoosporangia shown as ±, +, ++, +++ and ++++.

[2)] Subtropical strains (AN-1587, AN-1588), tropical strains (MT-88, MT-95).

Table 2. Zoosporangium formation of *H. porrigovesica* induced by submersion in seawater of 30 ppt at different temperatures.

	10	15	20	25	30	37(°C)
AN-1587[2)]	−[1)]	+	++	++++	+++	±*
AN-1588	−	±	+	++++	+++	±*
MT-88	−	−	−	+++	+++	++
MT-95	−	−	+	++	+++	+

* aborted

[1)] Relative abundance of produced zoosporangia shown as −, ±, +, ++, +++ and ++++.

[2)] Subtropical strains (AN-1587, AN-1588), tropical strains (MT-88, MT-95).

Table 3. Comparison of *H. porrigovesica* with other epapillate zoosporangium-forming species of *Halophytophthora* in asexual reproductive structures.

Species	Zoosporangiophore proliferation	Dehiscence plug-like material	Dehiscence pore	Vesicle
H. porrigovesica	no pattern	lens-shaped	inoperculate	cylindrical, extending at once
H. avicenniae	no pattern	cupulate	inoperculate	cylindrical, extending at once, with a small hemispherical annexed vesicle
H. kandeliae	sympodial	thin lens-shaped	operculate	spherical, pausing before release
H. operculata	sympodial	absent?	operculate	absent

ca, should be compared with these three in the detailed morphology of the asexual reproductive organs. *Halophytophthora avicenniae*, which has been isolated only from *Avicennia* leaves since its original description from Australia (Gerrettson-Cornell and Simpson, 1984), produces ovate to elliptical zoosporangia with a cup-shaped plug-like material at the apex. From Japanese mangroves, we also isolated this species from *A. marina* leaves. This species has a long cylindrical vesicle expanding prior to releasing zoospores, but also forms a small hemispherical annexed vesicle at the apex of the cylindrical vesicle (Nakagiri, pers. observation). *Halophytophthora kandeliae* forms operculate zoosporangia (Nakagiri, pers. observation), from which a spherical vesicle protrudes. The vesicle is persistent for more than 30 min before rupturing and releasing zoospores. The zoosporangia are formed successively on a sympodially proliferating zoosporangiophore. *Halophytophthora operculata* successively produces operculate zoosporangia in a sympodial manner, but they lack a vesicle at the opening. These characteristics clearly distinguish *H. porrigovesica* from the other three species (Table 3).

The following is a key to species of *Halophytophthora* species including the new species. Though species definition of *H. vesicula* and the similar species *H. batemanensis* (Gerr.-Corn. & J. A. Simpson) H. H. Ho & S. C. Jong and *H. polymorphica* (Gerr.-Corn. & J. A. Simpson) H. H. Ho & S. C. Jong requires further taxonomic studies (Nakagiri, 1993; Newell, 1992), they are included in the key (steps 7 and 8) and characterized by the original description.

KEY TO SPECIES OF *HALOPHYTOPHTHORA*

1. Sporangium papillate 2
1′. Sporangium epapillate 11
2. Sporangium with spines 3
2′. Sporangium smooth-walled 5
3. Spines short, 1–5 μm, clustering in groups and angled toward the center of the group; mycoparasitic ..... *H. mycoparasitica* (Fell & Master) H. H. Ho & S. C. Jong
3′. Spines long, 10–30 μm, distributed over whole surface of the zoosporangia or around papilla; saprophytic 4
4. Zoosporangium globose to ovate or obovate ..... *H. spinosa* (Fell & Master) H. H. Ho & S. C. Jong var. *spinosa*
4′. Zoosporangium multi-lobed or ovate ..... *H. spinosa* var. *lobata* (Fell & Master) H. H. Ho & S. C. Jong
5. Vesicle present 6
5′. Vesicle absent 9
6. Sporangial closure material including a solid plug (dehiscence plug) visible after ejection and persistent longer than 3 h ..... *H. masteri* Nakagiri & S. Y. Newell
6′. Sporangial closure material not including a solid plug (dehiscence plug-like material) vanishing at ejection 7
7. Zoosporangiophore proliferating sympodially ..... *H. vesicula* (Anastasiou & Churchl.) H. H. Ho & S. C. Jong
7′. Zoosporangiophore branching irregularly 8
8. Zoosporangium broadly elliptical to limoniform ..... *H. batemanensis* (Gerr.-Corn. & J. A. Simpson) H. H. Ho & S. C. Jong
8′. Zoosporangium polymorphic, frequently with a hollow lateral process ..... *H. polymorphica* (Gerr.-Corn. & J. A. Simpson) H. H. Ho & S. C. Jong
9. Dehiscence plug visible after ejection 10
9′. Dehiscence plug-like material liquescent, vanishing at ejection; zoosporangium sometimes externally proliferating ..... *H. exoprolifera* H. H. Ho, Nakagiri & S. Y. Newell
10. Dehiscence plug short, 3–7 μm, extruding through exit pore and protruded end ragged in appearance, semi-persistent less than 1 h after ejection ..... *H. bahamensis* (Fell & Master) H. H. Ho & S. C. Jong
10′. Dehiscence plug long, 10–50 μm, extruding through exit pore and protruded end convex, persistent at least several days ..... *H. epistomium* (Fell & Master) H. H. Ho & S. C. Jong
10″. Dehiscence plug intermediate, 10–22 μm, extending through exit pore and protruded end disintegrating or "cigarette-ash" shape, evanescing 1–5 min after ejection ..... *H. tartarea* Nakagiri & S. Y. Newell

Table 4. Preferred and optimal conditions for growth and asexual reproduction in subtropical and tropical strains of *H. porrigovesica*.

Strains	Hyphal growth		Asexual reproduction	
	Salinity	Temperature	Salinity	Temperature
Subtropical (Iriomote)	0–50 ppt	20–30°C	10–50 ppt	15–30°C
strains	opt. 30 ppt	opt. 25–30°C	opt. 30 ppt	opt. 25°C
Tropical (Thailand)	0–50 ppt	20–30°C	20–40 ppt	25–30°C
strains	opt. 30 ppt	opt. 30°C	opt. 30 ppt	opt. 30°C

11. Vesicle present 12
11′. Vesicle absent; zoosporangium operculate ..... *H. operculata* (Pegg & Alcorn) H. H. Ho & S. C. Jong
12. Vesicle spherical, retaining zoospores inside for a while before release; zoosporangium operculate ..... *H. kandeliae* H. H. Ho, H. S. Chang & S. Y. Hsieh
12′. Vesicle cylindrical, extending at once for zoospore release; zoosporangium inoperculate 13
13. Vesicle with a small, spherical annexed vesicle at the apex; dehiscence plug-like material cupulate ..... *H. avicenniae* (Gerr.-Corn. & J. A. Simpson) H. H. Ho & S. C. Jong
13′. Vesicle without an annexed vesicle; dehiscence plug-like material lens-shaped ..... *H. porrigovesica* Nakagiri, Tad. Ito, Manoch & Tanticharoen

Comparison of the subtropical (Iriomote) and tropical (Thailand) strains showed that they differ in the preferred conditions for the asexual reproduction, though there is no apparent difference in hyphal growth between them. The optimal temperature for zoosporangium formation is lower (25°C) in the subtropical strains than the tropical ones (30°C). The resistance to submersion in 37°C seawater in the asexual reproduction also indicates the tropical strains adapt well to higher temperature environments. These differences in reproductive properties apparently indicate an adaptation of the two types of strains to the climates of their own habitats. Moreover, the subtropical strains were shown to be adapted to wider ranges of salinity and temperature than the tropical strains (Table 4, summarizing Figs. 30, 31 and Tables 1, 2). These phenomena may be explained from the facts that the water salinity and temperature fluctuate greatly in the mangrove of a small river on a subtropical island according to the daily tidal rhythm and seasons, while they are more constant in the tropical mangroves of big rivers with huge deltas on a continent. Thus, the two types of strains are well adapted to the level and fluctuation range of the environmental conditions of their own mangrove habitats.

Taxon selectivity or host specificity is one of the elements expressing fungal diversity. In subtropical mangroves, *H. porrigovesica* has been isolated only from fallen leaves of *Sonneratia alba*, which grows at river mouths where salinity and water temperature are relatively high. On the other hand, in tropical mangroves this species has been found from submerged leaves of three species of mangrove trees, *S. alba, Bruguiera gymnorrhiza* and *Avicennia alba.* The former two inhabit mangroves in Iriomote Is., but *H. porrigovesica* has never been isolated from *B. gymnorrhiza* leaves by regular sampling over the past decade. Change of taxon selectivity with geographical distribution is known in saprophytic agarics (Rayner et al., 1985), and saprophytic microfungi (Tokumasu, 2000). The greater number of host species in the tropics and the preference of this species for higher temperature for growth and reproduction suggest that *H. porrigovesica* may have originally inhabited tropical mangroves. It is also inferred that the Iriomote strains have maintained an association with *S. alba* leaves and differentiated their properties to adapt to the environments of the subtropical habitats.

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