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PATHOGENESIS OF BRYOPHYTE HOSTS BY THE ASCOMYCETE *ATRADIDYMELLA MUSCIVORA*[1]

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Atradidymella muscivora (Pleosporales) is a bryophyte pathogen that infects the mosses *Aulacomnium palustre*, *Hylocomium splendens*, and *Polytrichum juniperinum*. Light and scanning electron microscopy and extracellular enzyme production were used to characterize the interactions between this fungus and its native hosts and the model host *Funaria hygrometrica.* Penetration was direct via hyphae or appressoria, and hosts responded by forming layered, darkly pigmented deposits at penetration sites, similar to the papillae formed by vascular plants in response to fungal infection. Infected hosts gradually became chlorotic as hyphae grew intracellularly, presumably killing host cells. Pycnidia of the *Phoma* anamorph (*P. muscivora*) and uniloculate pseudothecia were initiated as tightly packed masses of stromatic dematiaceous hyphae within a single host cell. Mature pycnidia and pseudothecia were erumpent. A new microniche among bryophilous fungi is described, whereby *A. muscivora* supplants the gemmae of *Aul. palustre* and exploits the normal nutrient-flow of the moss gametophyte. *Atradidymella muscivora* produced both cellulases and soluble polyphenolic oxidases, allowing it to also function as a saprobe and degrade the cell walls of bryophytes. The saprophytic and pathogenic abilities of *A. muscivora* suggest it may play a role in nutrient cycling, population dynamics, and small-scale disturbances in boreal ecosystems.

Key words: bryophilous; cell wall degradation; host response; microniche; papilla; pathogenesis; *Phoma muscivora*; stroma reduction.

Fungal pathogens of mosses have been reported since the mid 19th century (Racovitza, 1959) and are posited to play important roles in nutrient cycling, population dynamics, and small-scale disturbances that alter community composition in bryophyte-dominated ecosystems (Davey and Currah, 2006). Host chlorosis and necrosis, the general symptoms of fungal pathogenesis of bryophytes, are well documented (Wilson, 1951; Hawksworth, 1973; Redhead, 1981; Tsuneda et al., 2001a; Döbbeler, 2003). Great diversity in host cell penetration and disruption, mechanisms of obtaining nutrients, host responses, and disease etiology has been observed among bryophyte pathogens (Döbbeler, 1997; Davey and Currah, 2006), and some species are highly specialized for their bryophilous habit (Döbbeler, 1997). However, only a limited number of bryophilous pathogens and the diseases they cause have been comprehensively studied. Of these, most are basidiomycetes, including *Eocronartium muscicola* (Pers.) Fitzp. (Boehm and McLaughlin, 1988), *Arrhenia retiruga* (Bull.) Redhead (Hassel and Kost, 1998), and *Tephrocybe palustris* (Peck) Donk (Redhead, 1981; Untiedt and Müller, 1985). Although ascomycete pathogens of bryophytes have been reported and symptoms of infection are often well documented (Racovitza, 1959), only *Scleroconidioma sphagnicola* Tsuneda, Currah & Thormann (Tsuneda et al., 2001a) has been characterized thoroughly using modern microscopic techniques.

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Atradidymella muscivora Davey & Currah is a pathogen of mosses that produces a *Phoma* anamorph (*P. muscivora*) and has phylogenetic affinities to the *Phoma-Ascochyta-Didymella* complex that is sister to the Phaeosphariaceae in the Pleosporales (Davey and Currah, 2009, in this issue). Members of this complex are well known as saprotrophs, parasites, and pathogens of vascular plants (Corlett, 1981; Schoch et al., 2006) and species of *Phoma*, *Ascochyta*, and *Didymella* have previously been reported from bryophytes and hepatophytes (Racovitza, 1959; Döbbeler, 1978; Kerry, 1990; Möller and Dreyfuss, 1996; Tosi et al., 2002; Thormann and Rice, 2007). Using light and scanning electron microscopy and extracellular enzyme profiling, we characterized the pathogenesis of *A. muscivora* infecting the model host *Funaria hygrometrica* and observed the interactions between *A. muscivora* and its natural hosts.

MATERIALS AND METHODS

Host–fungus interactions—The model host *Funaria hygrometrica* Hedw. and the native hosts *Polytrichum juniperinum* Hedw. and *Hylocomium splendens* (Hedw.) Schimp. were cultured from spores on White's basal salt media (Sigma) solidified with 15 g Phytagel/L media (Sigma) in 100 mL glass tissue culture vessels with vented Magenta B-cap closures (Sigma) as described in Davey and Currah (2007). Another native host, *Aulacomnium palustre* (Hedw.) Schwaegr., was cultured in vitro from gemmae that were surface sterilized in 1 mL of 1% NaOCl for 3 min with agitation by vortexing, and then washed three times in 1 mL of sterile distilled water for 1 min. The surface-sterilized gemmae were suspended in sterile distilled water and cultured in the same manner as described for the spores. Gametophytes of the five-leaf stage were inoculated with isolates of *Atradidymella muscivora* (UAMH 10909, 10910, 10911, Ap1-S, Ap1-Q) by placing 5-mm-diameter plugs taken from near the margin of 15–30-d-old colonies grown on oatmeal agar (OA: 20 g/L agar [Invitrogen, Carlsbad, CA, USA], 20 g/L ground oatmeal) and placing them among the gametophytes and in contact with both leaves and rhizoids. The inoculated gametophytes and uninoculated control gametophytes were incubated for 12 wk and observed with light microscopy (LM) weekly. Important stages in the pathogenesis were selected for further examination by LM and scanning electron microscopy (SEM). The fungus was reisolated from hosts infected in vitro and its identity reconfirmed to satisfy Koch's postulates.

Microscopy—Health of gametophytes was examined with a stereomicroscope and by mounting individual leaves or entire gametophytes in water or

polyvinyl alcohol with acid fuchsin (0.05 g acid fuchsin in 10 mL lactic acid and 1 mL glycerine mixed with 1.66 g polyvinyl alcohol dissolved in 10 mL water) and examining them at 40–100× magnification with a compound microscope. Infected host tissues were fixed in FAA (10 mL 40% formaldehyde, 50 mL ethanol, 5 mL acetic acid, 35 mL water) or 2% glutaraldehyde (Sigma, St. Louis, Missouri, USA) in Millonig's buffer (pH 7.5) (Millonig, 1961) for a minimum of 24 h, dehydrated in an ethanol series, and embedded in paraffin wax. Sections were stained using safranin O (Sigma), counterstained with fast green FCF (Sigma), and mounted using DPX mountant (Sigma). Light micrographs of all preparations were taken using an Olympus BX50 microscope with a DP-12 digital camera (Olympus, Tokyo, Japan).

For SEM, infected gametophytes were fixed in 2% glutaraldehyde overnight. Fixed gametophytes were rinsed in distilled water and placed in 2% tannic acid–2% guanidine hydrochloride (Sigma) solution for 4–5 h and then postfixed overnight in 2% OsO_4 (Sigma) at 5°C. Fixed material was dehydrated in ethanol series, taken to amyl acetate, and critical-point dried in a BAL-TEC CPD 030 dryer (BAL-TEC, Balzers, Liechtenstein) using carbon dioxide. Dried samples were coated with gold and examined with a Hitachi (Tokyo, Japan) S-510 scanning electron microscope at 10 or 15 kV.

Enzyme characterization—Three strains of *Atradidymella muscivora* (Ap1-Q, UAMH 10909, 10911) were tested for amylase, gelatinase, pectinase, cellulase, lipase, and insoluble and soluble polyphenolic oxidase enzyme activities using indicator media, as described by Davey and Currah (2007).

RESULTS

Atradidymella muscivora was repeatedly isolated from collected material (Davey and Currah, 2009, this issue), as well as from hosts inoculated in vitro. Preliminary LM examinations of *A. muscivora* infecting all four host species indicated that virulence and host responses were similar among the native hosts and model host. Therefore, detailed characterization was limited to *Funaria hygrometrica*.

***Infection of* Funaria hygrometrica**—Initial stages of infection (1–10 d) by *A. muscivora* were characterized by the production of floccose, white aerial mycelium on the surface of the gametophytes followed by attempted penetration of rhizoids, leaves, and protonemata. Ingress into the host occurred as early as 5 d post-inoculation, and was either by direct penetration of cell walls by vegetative hyphae (Fig. 1) or by penetration pegs produced by dome-shaped, swollen appressoria, that differentiated both laterally and terminally from vegetative hyphae (Figs. 2, 3). A thickened, pigmented, papilla-like deposit in the host cell frequently surrounded the penetrating hyphae (Figs. 2, 4). These papilla-like deposits were simple, bifurcate, or stellate (Fig. 2) depending on the branching pattern of the intruding hypha. Successful penetration was observed both in the absence of the host response and when hyphae or penetration pegs were able to grow through the papilla-like deposits. Hyaline, intracellular hyphae, 1–2.5 μm in diameter, were observed after 5–20 d (Fig. 5), and the infected leaf and rhizoid cells contained few or no chloroplasts (Figs. 6, 7). Intracellular hyphal growth between adjacent cells frequently elicited a host response at the location where the hypha traverses the cell wall. Eventually, leaves of infected gametophytes became chlorotic and mottled with necrotic cells and darkly pigmented spots where the host response had occurred (Figs. 8, 9). Cell wall degradation was limited to areas invaded by hyphae of *A. muscivora* and was evidenced by hyphae growing between the lamellate layers of the host cell wall and by general thinning of the cell wall that resulted in the formation of localized voids (Figs. 10–12). By comparison, cell walls of the controls were smooth and of uniform thickness, with intact lamellate layers.

Pycnidia formed on the gametophyte after 7–20 d and were initiated primarily within leaf and stem tissues and less frequently within rhizoids. Pycnidial initials were produced intracellularly, each originating as a tightly packed, dematiaceous, hyphal proliferation within a single cell of a leaf, rhizoid, or stem (Figs. 13–15). Subsequent enlargement of the hyphal mass and development of the pycnidium caused the cell to rupture, and the pycnidium enlarged at the surface of the gametophyte (Figs. 16–19). Pseudothecium development was analogous to pycnidium development, with stromata initials being produced intracellularly within a single cell that was ultimately ruptured by the developing pseudothecium (Figs. 20–22). Conidia were exuded in slimy droplets from the pycnidia (Fig. 19), while active release of ascospores from pseudothecia was not observed, and ascospores were left free within the pseudothecium (Fig. 22) after the ascus walls deliquesced.

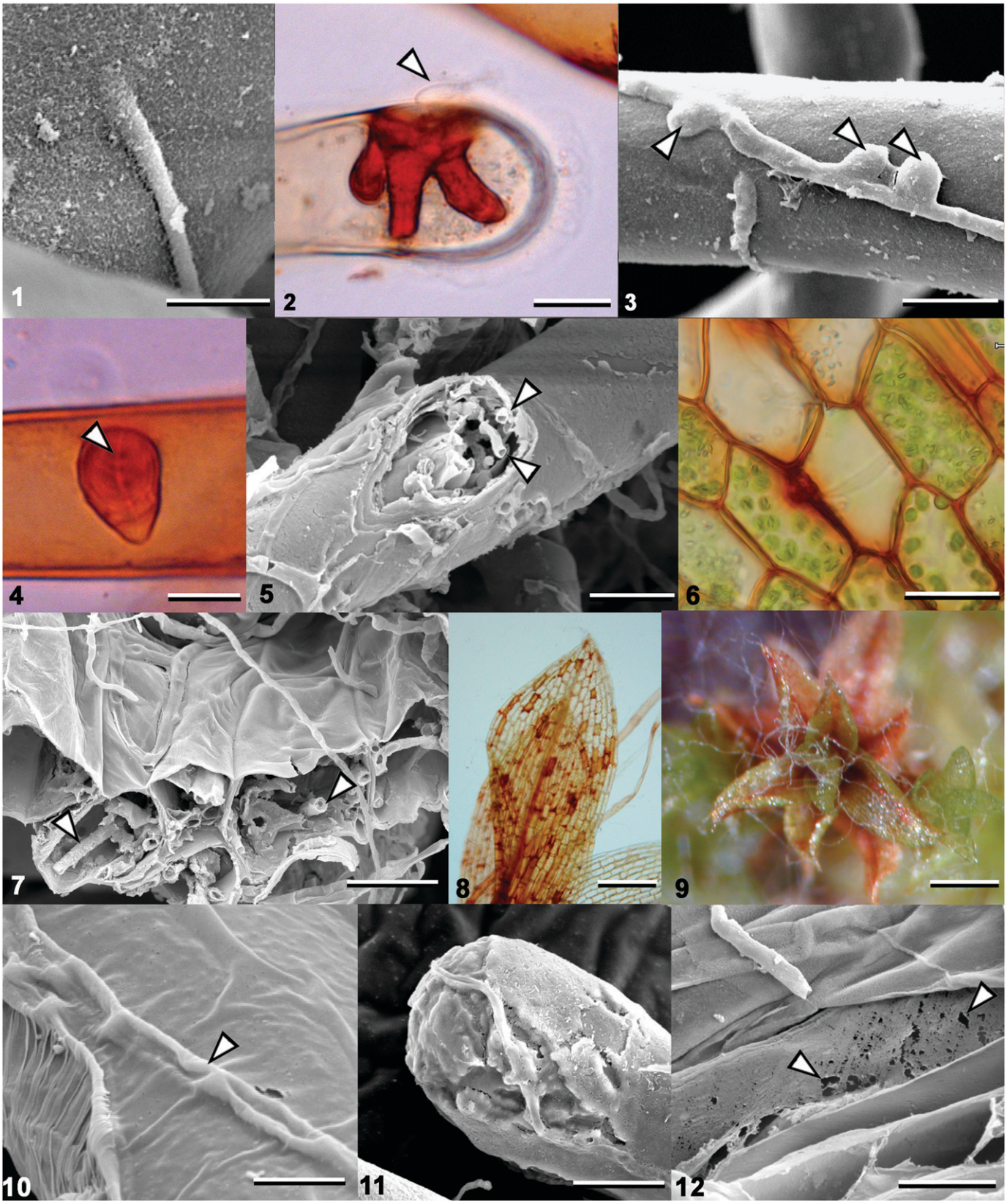
Infection of natural hosts—Initial stages of infection of *H. splendens* and *Aul. palustre* by *A. muscivora* were identical to those in *F. hygrometrica*. Host penetration occurred directly via vegetative hyphae or appressoria (Fig. 23), and both hosts responded by depositing layers of darkly pigmented material around penetration sites and invading hyphae (Fig. 24). As observed in *F. hygrometrica*, hyphae grew intracellularly, and penetration of a new cell frequently elicited a host response (Fig. 28). Production of pycnidia within single host cells was consistent between *Funaria*, *Aulacomnium*, and *Polytrichum* (Figs. 25, 29). However, in *Aulacomnium*, pycnidia formed primarily in cells of gemmae and at the gemma axils (Figs. 26–29). In *Polytrichum*, pycnidia frequently formed in the photosynthetic lamellae cells of the leaves or in the protective, hyaline cells of the leaf margin. Cell wall degradation in all three natural hosts was similar to that observed in the *A. muscivora–F. hygrometrica* model system (Figs. 30, 31).

Enzyme activity and cell wall degradation—All isolates tested negatively for amylase, pectinase, lipase, and insoluble polyphenolic oxidase activities. Tests for cellulase, gelatinase, and soluble polyphenolic oxidase activities were positive in all isolates.

DISCUSSION

Atradidymella muscivora causes chlorosis, necrosis, and sometimes death of its hosts, indicating it is a pathogen of mosses. The fungus appears to be a generalist pathogen with a broad host range among temperate mosses; it has been isolated from three different genera representing three bryophyte orders (Polytrichales, Hypnales, Bryales) (Davey and Currah, 2009, this issue) and also readily infects the model host *F. hygrometrica* (Funariales).

The disease cycle of *A. muscivora* is initiated with host penetration, with or without the formation of appressoria. Positive tests for cellulase and soluble polyphenolic oxidase activity indicate that penetration probably involves some degree of lytic dissolution of the host cell wall. *Funaria hygrometrica*, *Aul. palustre*, and *H. splendens* respond to the intruding hyphae by depositing layers of darkly pigmented material around them, ultimately forming a structure resembling the callose- and polyphenolic-rich papillae formed by vascular plants in response to penetration attempts by parasitic and pathogenic fungi (Aist, 1976; Cole and Hoch, 1991.) Bifurcate and stellate papillae indicate that the fungus may be responding to initial



Figs. 1–12. Colonization and degradation of *Funaria hygrometrica* by *Atradidymella muscivora*. Figs. 1, 3, 6, 8: UAMH 10911; Figs. 2, 4: Ap1-Q; Figs. 5, 7, 9–12: UAMH 10909: Figs. 1, 3, 5, 7, 10–12: SEM; Figs. 2, 4: = lactofuchsin mount; Figs. 6, 8: wet mount. **1.** Vegetative hypha directly penetrating host rhizoid. Scale bar = 10 μm. **2.** Tip of protonematal filament colonized by *A. muscivora.* The fungus produced an appressorium (white arrowhead)

host defenses by branching in an attempt to avoid or escape from the papilla. Papilla formation has previously been reported in *Funaria hygrometrica* (Martínez-Abaigar et al., 2005) and a taxonomically diverse suite of mosses infected by basidiomycetes and ascomycetes (Racovitza, 1959; Hassel and Kost, 1998). Similar responses have been described in both hepatophytes (Racovitza, 1959; Read et al., 2000) and angiosperms (Aist, 1976; Cole and Hoch, 1991), suggesting that it is a generalized, early-evolved host response that may be common to all major plant lineages, similar to the salicylic-acid-induced defense responses that have been described in the moss *Physcomitrella patens* and a wide variety of vascular plants (Andersson et al., 2005).

Host cells that have been successfully penetrated by *A. muscivora* lack chloroplasts. It is unknown whether *A. muscivora* produces a chloroplast-degrading phytotoxin, but other members of the Phaeosphaeriaceae and *Phoma-Ascochyta-Didymella* clade to which *A. muscivora* is evolutionarily close (Davey and Currah, 2009, this issue) are known to produce a variety of phytotoxins (Pedros and Chumala, 2005; Vikrant et al., 2006), including calmodulin-inhibiting enolides that can interfere with photosynthesis (Rivero-Cruz et al., 2003). The patterns of cell wall degradation and the ability of *A. muscivora* to degrade both cellulosic and polyphenolic cell wall components suggest that the fungus does not obtain its nutrients solely from the cytoplasmic contents of its host and can also function as an opportunistic saprobe on dead material. While the generalized thinning and formation of localized pits that appear in gametophytes infected with *A. muscivora* have previously been observed in the degradation of *Sphagnum fuscum* by *Oidiodendron maius* (Myxotrichaceae, Leotiomycetes) (Tsuneda et al., 2001b), the patterns of cell wall degradation of polytrichalean mosses by ascomycetes have not been similarly investigated. Further investigation is needed to determine if other ascomycetous saprobes of polytrichalean mosses, such as *Aphanotria paradoxa* (Döbbeler, 2007), exhibit cell wall decomposition patterns similar to those of *A. muscivora.*

After successful host penetration and colonization, pycnidia and pseudothecia of *A. muscivora* are initiated, each within a single cell, and both structures subsequently erupt from the underlying host cell. The fungus' lack of pectinolytic enzymes to aid in intercellular growth via the breakdown of the middle lamella, in conjunction with the initiation of a host response each time a cell is penetrated likely increases the energetic cost of forming a large stroma involving multiple host cells. This combination of factors may have created evolutionary pressure for stroma reduction and the compartmentalization of the reproductive stages of *A. muscivora* into single host cells. Highly reduced reproductive structures that are limited to a single host cell have been reported among other bryophilous and hepaticolous fungi with various taxonomic affinities (Racovitza, 1959; Döbbeler, 1980), suggesting that such reduction allows for specialization to a bryophyte host and has multiple origins among bryophilous fungi.

The ability of *A. muscivora* to produce rapidly a sporulating asexual state is likely integral to its persistence on a moss host, because many species occurring in the boreal zone, including *Hylocomium splendens* and *Polytrichum juniperinum,* are poikilohydric and frequently dry out, becoming osmotically inhospitable and having little metabolic activity (Proctor and Tuba, 2002). The rapid production of pycnidia would allow *A. muscivora* to exploit periods of wet weather for dispersal and colonization of new hosts, effectively perpetuating the disease cycle. Conidia formed in a slimy droplet or cirrhus are most conducive to dispersal by water. This feature may be adaptive by ensuring that conidia are dispersed during periods suitable for germination, thus maximizing potential for infection. The lack of active spore dispersal and retention of most ascospores in the pseudothecium suggests that the teleomorph functions primarily to introduce and maintain genetic variability. The entire ascoma of *A. muscivora* may then function as a diaspore or that the ascospores may be dispersed by mechanical disruption of the ascocarp or passively dispersed during successive drying and rehydration cycles in the same manner ascospores are passively extruded in some hypocrealean species (Rossman et al., 1999). Finally, it is possible that, in *Aulacomnium palustre* infected by *A. muscivora*, the fungus and its host form a common diaspore and that the gemmae colonized by the fungus are dispersed, much in the same way the hepaticolous basidiomycete *Gerronema pseudogrisellum* is dispersed with its host's gemmae (Redhead, 1980).

Atradidymella muscivora exhibits some microniche specialization on its native hosts, forming pycnidia preferentially on the leaf lamellae and along the involute leaf margins of *Pol. juniperinum,* and on or in the axils of gemmae in *Aul. palustre*. In *Pol. juniperinum*, the relatively large quantities of photosynthate produced by the lamellae and the narrow spaces between them would provide ample resources and a sheltered location for pycnidium production. The nutrient-rich gemmae of *Aul. palustre*, which are modified leaves, present a similar rich microniche for the formation of fungal reproductive structures. In this position, the incipient fungal sporocarps ostensibly intercept and absorb nutrients that would otherwise go to the formation of the host's vegetative propagules. This microniche is comparable to the bryophilous basidiomycete *Eocronartium muscicola*, which parasitizes gametophyte transfer cells, intercepting nutrients destined for sporophyte production and diverting them to the formation of the parasite's basidiomata (Boehm and McLaughlin, 1988), and *Calonectria frullaniae*, a hepaticolous ascomycete whose ascomata also replace the developing host sporophytes (Döbbeler, 2002). A similar co-opting of host resources may occur in species of *Lizonia* that preferentially colonize the reproductive apices of their hosts' gametophytes (Racovitza, 1959; Döbbeler, 2003).

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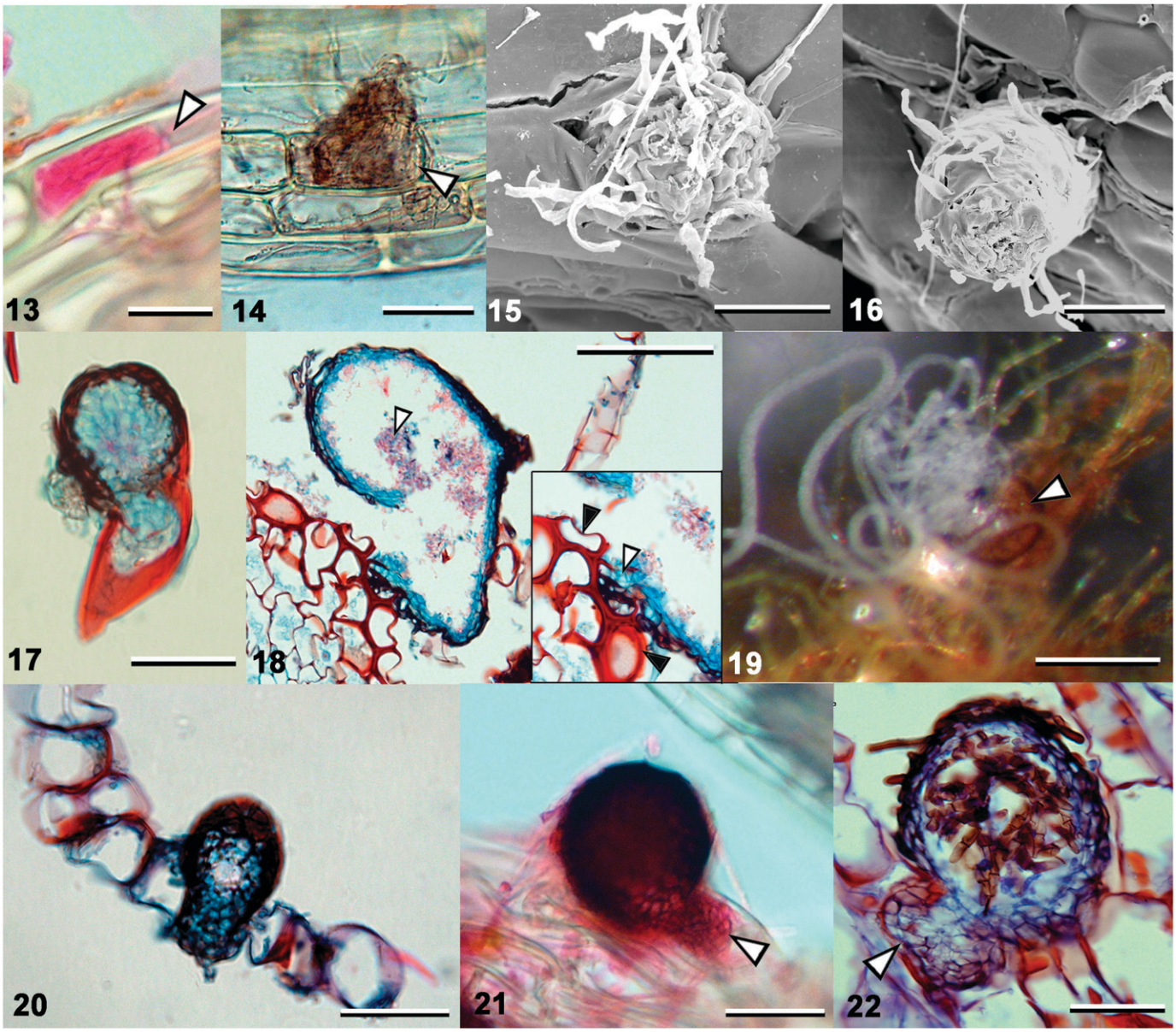
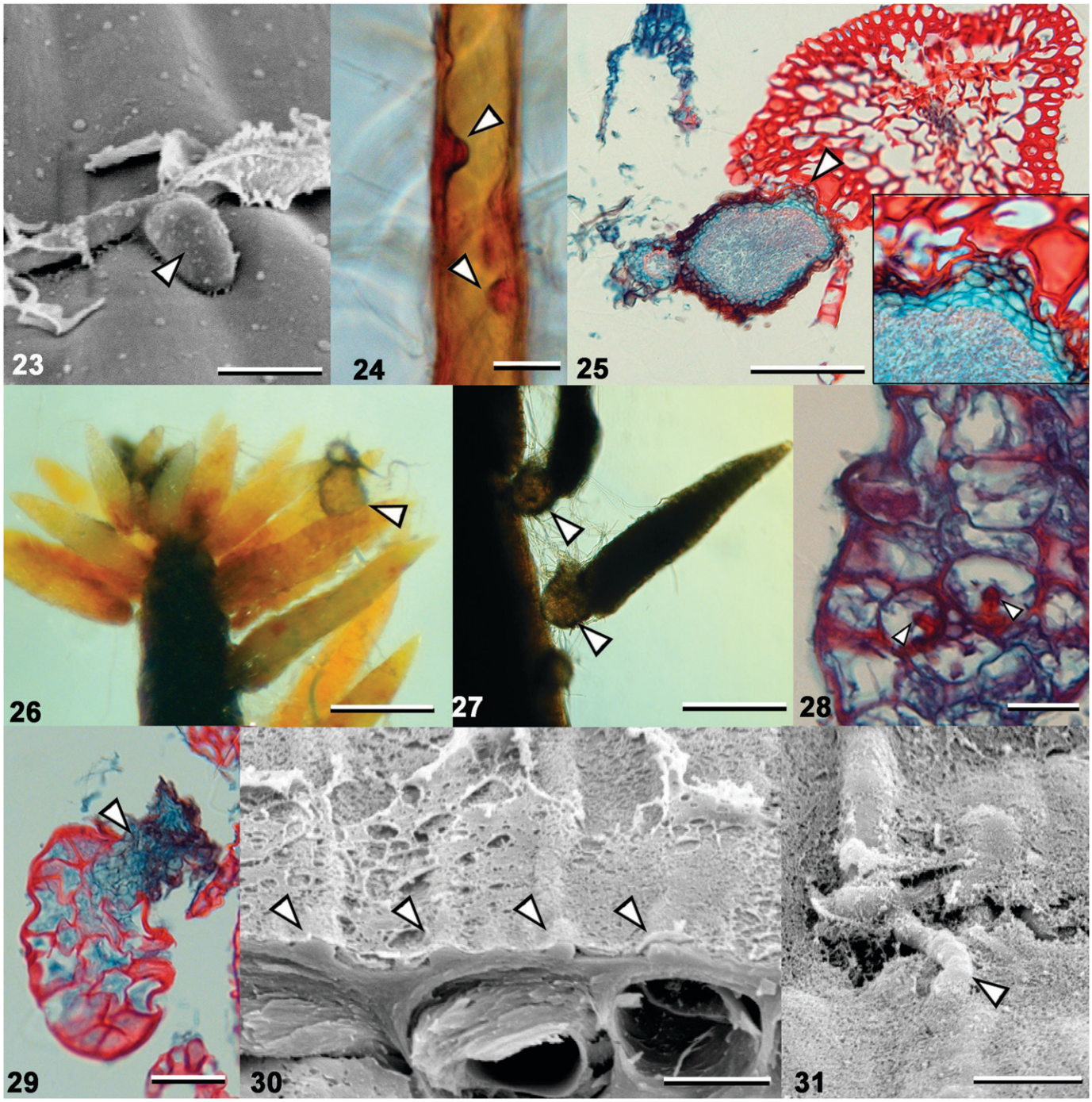
to facilitate host penetration. The host has responded to the attempt by depositing darkly pigmented materials (papilla) around the intruding hyphae. Scale bar = 10 μm. **3.** Appressoria (arrowheads) on a host rhizoid. Scale bar = 10 μm. **4.** Rhizoid with a papilla formed in response to a penetration attempt. Penetrating hypha is indicated by an arrowhead. Scale bar = 5 μm. **5.** Rhizoid colonized by *A. muscivora*. A branch of the rhizoid has been broken off, exposing lamellate cell wall layers and intracellular hyphae (arrowheads). Scale bar = 20 μm. **6.** Chlorotic leaf cells infected by *A. muscivora*. Scale bar = 20 μm. **7.** Leaf in cross section showing cells containing hyphae (arrowheads). Scale bar = 12 μm. **8.** Heavily infected *Funaria* leaf that has become chlorotic and mottled due to host response. Scale bar = 400 μm. **9.** Mottled, chlorotic gametophyte infected with *A. muscivora*. Scale bar = 1 mm. **10.** Hypha (arrowhead) seen in outline growing just below the surface of the host cell wall, between the lamellate layers. Scale bar = 5 μm. *Note:* Lamellations of cell wall are visible in cross section in Fig. 5. **11.** Rhizoid tip infected by *A. muscivora* showing generalized wall thinning. Scale bar = 13 μm. **12.** *Funaria* leaf cell with localized voids (arrowheads) where the cell wall material has been degraded. Scale bar = 10 μm.



Figs. 13–22. Development of pycnidia and pseudothecia of *Atradidymella muscivora* on the model host *Funaria hygrometrica*. (Figs. 13–15, 18, 21, 22: UAMH 10909; Figs. 16, 17, 19–20: UAMH 10911; Figs 13, 21: lactofuchsin mount; Figs. 14, 19 = wet mount; Figs. 15, 16: SEM; Figs. 17, 18, 20, 22 = paraffin section stained with safranin O-fast green FCF) **13.** Leaf cell containing tightly packed, pink-stained hyphae (arrowhead) of *A. muscivora*. Scale bar = 35 μm. **14.** Young pycnidium (arrowhead) emerging from leaf cell. Scale bar = 40 μm. **15.** Young pycnidium of *A. muscivora* (UAMH 10909) emerging from stem cell. Scale bar = 17 μm. **16.** Maturing pycnidium on a leaf of *Funaria.* Scale bar = 20 μm. **17.** Longitudinal section of young pycnidium erumpent from rhizoid. Scale bar = 25 μm. **18.** Section of infected stem of *Funaria* bearing a single, erumpent pycnidium containing masses of conidia (arrowhead). Scale bar = 85 μm. Inset, entire pycnidium erupting from a single cell (white arrowhead); adjacent cells are not disrupted (black arrowheads). **19.** Mature pycnidium (arrowhead) releasing a cirrhus of conidia into distilled water. Scale bar = 150 μm. **20.** Cross section of a developing stroma erumpent from a leaf cell. Scale bar = 30 μm. **21.** Young pseudothecium and stroma (arrowhead). Scale bar = 30 μm. **22.** Longitudinal section of mature pseudothecium showing jumbled mass of unliberated ascospores within the pseudothecium and stroma contained within a single host cell (arrowhead). Scale bar = 35 μm.

Although *A. muscivora* has many structural features common to plant pathogenic fungi, its pathogenesis is unique when compared to previously characterized fungal pathogens of bryophytes. Both ascomycete and basidiomycete pathogens have been reported to penetrate bryophyte hosts directly via hyphae or appressoria (Racovitza, 1959; Kost, 1988; Döbbeler, 1997), although *A. muscivora* represents the first report of concurrent lytic and mechanical penetration. Papilla induction in host cells has been observed in other bryophilous ascomycetes including *Nectria muscivora* and *Teichospora jungermannicola* (Racovitza, 1959) and in basidiomycetes such as *Galerina paludosa* (Redhead, 1981), *Arrhenia retiruga* (Hassel and Kost, 1998), and *Rickinella fibula* (Kost, 1988). However, in these examples, the host response is associated with primary penetration



Figs. 23–31. Infection of *Aulacomnium palustre*, *Hylocomium splendens*, and *Polytrichum juniperinum* by *Atradidymella muscivora*. Fig. 23: UAMH 10910; Fig. 24: Ap1-Q; Figs. 25–29: Ap1-S; Figs. 30, 31: UAMH 10909; Figs. 23, 30, 31: SEM; Fig. 24: lactofuchsin mount; Figs. 25, 28, 29: paraffin section stained with safranin O–fast green FCF; Figs. 26, 27 = wet mount) **23.** Appressorium on leaf cell of *Hylocomium*. Scale bar = 6 μm. **24.** Rhizoid of *Aul. palustre* that has formed papillae (arrowheads) in response to penetration attempts. Scale bar = 10 μm. **25.** Cross section of stem of *Aul. palustre* showing pycnidium emerging from epidermal cell (arrowhead). Scale bar = 75 μm. Inset, enlarged view of pycnidium emerging from cell. **26.** Apex of gemma stalk of *Aul. palustre* with pycnidia (arrowhead) on its gemmae. Scale bar = 650 μm. **27.** Gemma stalk of *Aul. palustre* showing pycnidia (arrowheads) emerging from stem cells and replacing the gemmae. Scale bar = 250 μm. **28.** Longitudinal section of heavily infected gemma of *Aul. palustre* with papilla formed in response to intracellular hyphal growth. Scale bar = 20 μm. **29.** Oblique section of gemma of *Aul. palustre* showing pycnidium emerging from a cell (arrowhead). Scale bar = 50 μm. **30.** Abaxial side of leaf of *Pol. juniperinum* with hyphae (arrowheads) growing between the lamellate layers of the cell wall. Scale bar = 20 μm. **31.** Leaf cell of *Pol. juniperinum* with generalized wall thinning and localized voids formed around an invading hypha (arrowhead). Scale bar = 10 μm.

attempts rather than with intracellular hyphal growth, as observed in *A. muscivora*.

In summary, *A. muscivora* is a generalist pathogen of mosses, whose life cycle, morphology, and patterns of host and microniche exploitation all show specific adaptations to the bryophyte host. Further detailed studies of pathogen–host interactions among an untold diversity of bryophilous fungi and their hosts is expected to illustrate consistent etiologic patterns among fungal plant pathogens along with a wealth of unique adaptive strategies. Further in vivo studies of this generalist pathogen are needed to determine what role it plays in the population dynamics of its bryophyte hosts and whether it can create small-scale disturbances within the boreal ecosystems in which it is found.

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