Schizolysis of dolipore–parenthesome septa in an arthroconidial fungus associated with *Dendroctonus ponderosae* and in similar anamorphic fungi[1]

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An arthroconidial anamorphic fungus occurred in pupal chambers of the mountain pine beetle (*Dendroctonus ponderosae*) in lodgepole pine. No teleomorph was found and no suitable form genus was available for its disposition. However, in cultural characteristics it closely resembled the group 1 arthroconidial fungi, defined by other researchers as probable basidiomycete anamorphs. Septa of the pupal-chamber fungus and several of the group 1 isolates were of the dolipore–parenthesome type. Conidial separation was by septum schizolysis. Cell separation was initiated by disintegration of the dolipore wall, followed by progressive shrinkage of the fused dolipore wall. The parenthesomes retracted towards the dolipore wall and the triangular areas of the cross wall dissolved. The cross wall then split centripetally along the median electron-light layer to complete cell separation. The pupal-chamber fungus was also compared with *Phlebia radiata* (group 2) and with groups 3 and 4 strains of other researchers. *Mauginiella scaettae* was confirmed to have simple septa; thus this genus fails to accommodate arthroconidial basidiomycete anamorphs.

Key words: basidiomycete anamorphs, dolipore–parenthesome septa, septum schizolysis, arthroconidiogenesis, *Phlebia radiata*, *Mauginiella scaettae*.

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Dans les loges des pupes du *Dendroctonus ponderosa* sur le pin lodgepole, on retrouve un champignon arthroconidien anamorphe. Pour en disposer, aucun téléomorphe n'a été retrouvé non plus que de genre de forme. Cependant, ses caractéristiques culturales le rapproche du group 1 de champignons arthroconidiens, défini par d'autres chercheurs comme des anamorphes probables de basidiomycètes. Les septations du champignon des loges de pupes et plusieurs isolats du groupe 1 sont du type à dolipore et parenthésome. La séparation des conidies se fait par schizolyse de la septation. La séparation cellulaire débute par la désintégration de la paroi du dolipore, suivie d'un repli progressif de la paroi du dolipore fusionnée. Les parenthésomes se rétractent vers la paroi du dolipore et les surfaces triangulaires de la paroi transverse se dissolvent. La paroi transverse se fend alors de façon centripète, le long de la couche médiane transparente aux électrons, pour compléter la séparation cellulaire. Le champignon de la loge de la pupe a été également comparé avec le *Phlebia radiata* (group 2) ainsi qu'avec les souches des groupes 3 et 4 défini par d'autres chercheurs. Le *Mauginiella scaettae* comporte des septations simples; conséquemment ce genre ne peut pas accommoder les anamorphes arthroconidiens de basidiomycètes.

Mots clés : anamorphes de basidiomycètes, septations à dolipore et parenthésome, schizolyse des septations, arthroconidiogénèse, *Phlebia radiata*, *Mauginiella scaettae*.

[Traduit par la rédaction]

Introduction

During our investigation of fungi associated with the mountain pine beetle (*Dendroctonus ponderosae* Hopk.) in lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.), we found an arthroconidial fungus in some pupal chambers. Although this fungus resembled *Geotrichum* Link in forming arthroconidia by schizolytic dehiscence (Cole and Samson 1979; Tsuneda 1987; Tsuneda and Murakami 1989), it differed in that its conidia were dry rather than slimy. Further, our preliminary ultrastructural study revealed that the pupal-chamber fungus possessed dolipore–parenthesome septa unlike *Geotrichum*, which has multiperforate septa (Hashimoto et al. 1964; Kreger-van Rij and Veenhuis 1974; de Hoog et al. 1986; Tsuneda and Murakami 1989). The teleomorphs of *Geotrichum* are in the ascomycetous genera *Dipodascus* Lagerheim and *Galactomyces* Redhead & Malloch (de Hoog et al. 1986).

Sigler and Carmichael (1976), in their article on the *Malbranchea* complex, described some arthroconidial anamorphs with presumed affinities to Hymenomycetes. Two groups of isolates formed dry, randomly developed, schizolytic arthroconidia, and they questioned whether the form genus *Mauginiella* Cavara might be appropriate for their disposition. None of the strains included in their group 1 could be linked to a teleomorph, whereas both strains in group 2 were received from the Centraalbureau voor Schimmelcultures, Baarn, The Netherlands, as *Phlebia radiata* Fr. Their group 3 was characterized by the presence of narrow separation cells between maturing arthroconidia, and group 4 by the development of alternate arthroconidia. Our pupal-chamber fungus appeared to fit well within the group 1, but its affinity to *Mauginiella* was doubtful because the type species of this genus, *M. scaettae* Cavara,

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TABLE 1. Arthroconidial basidiomycete anamorphs examined in this study, all of which have a dolipore–parenthesome septum

Isolate No.	Group No.[a]	Source	Secession[b]
UAMH 448	1	Human skin from perianal region	S
UAMH 2098	1	Ascoma of *Hypoxylon mummularium*	S
UAMH 3251	1	Human urine	S
UAMH 4014	1	Alfalfa roots	S
UAMH 4259	1	Rust gall of *Endocronartium harknessii*	S
UAMH 4919	1[c]	Pupal chamber of *Dendroctonus ponderosae*	S
TMI 1359	2	*Phlebia radiata*: mycelium of a basidioma	S
UAMH 645	3	Human toes	S or R
UAMH 514	4	Human blood	S or R

[a] After Sigler and Carmichael (1976).
[b] S, schizolytic secession; R, rhexolytic secession.
[c] Tentatively assigned based on the results of this study.

was reported to have cell walls and septa characteristic of ascomycetes (von Arx et al. 1981).

In a review of conidial types in the basidiomycetes, Kendrick and Watling (1979) showed that thallic-arthric conidia, formed by simple disarticulation of hyphae, were one of the commonest types of conidia in the Hymenomycetes. Two types of secession are recognized: (*i*) schizolytic secession in which a double septum between adjacent conidia separates centripetally as a result of lytic enzyme activity, and (*ii*) rhexolytic secession in which the periclinal wall of alternate segments of the fertile hyphae ruptures or lyses (Cole and Samson 1979; Hughes 1979). Arthroconidial basidiomycetes can be isolated from various substrates, including clinical specimens, but for many of these isolates their connections to teleomorphs are unknown.

The purpose of this study was to compare the pupal-chamber isolate with selected isolates from groups 1–4 as well as with *M. scaettae* by examining the ultrastructure of the septum and the mechanism of arthroconidium development and dehiscence.

Materials and methods

The fungal isolates used in this study are listed in Table 1. In addition, a strain of *M. scaettae* (UAMH 4291; University of Alberta Microfungus Collection and Herbarium, Edmonton, Alta.) was examined for comparison. All of these fungi were grown on 2% malt extract agar (Difco, Detroit, Mich.) or potato dextrose agar (Difco) at 20°C in the dark. Fungal material was removed from the cultures and examined by light (LM), scanning (SEM), and transmission electron microscopy (TEM). Fungal nuclei were stained by the HCl–Giemsa method after Aist (1969). For SEM, 5-mm agar discs bearing fungal material were cut from the cultures, washed in phosphate buffer (pH 7.0, Wako, Osaka, Japan) and fixed in 3% glutaraldehyde in buffer for 2–4 h at 5°C. After rinsing with buffer, these discs were immersed in 2% tannic acid – 2% guanidine hydrochloride solution for 4 h or longer at 5°C. The discs were then washed in distilled water and postfixed overnight in 2% OsO_4 at 5°C. The fixed material was dehydrated in an ethanol series, taken to amylacetate, and critical point dried in a Hitachi HCP-2 unit using carbon dioxide. The dried samples were coated with gold–palladium and examined with a Hitachi S-800 scanning electron microscope. The method used in preparation of material for TEM was the same as described previously (Tsuneda and Murakami 1985).

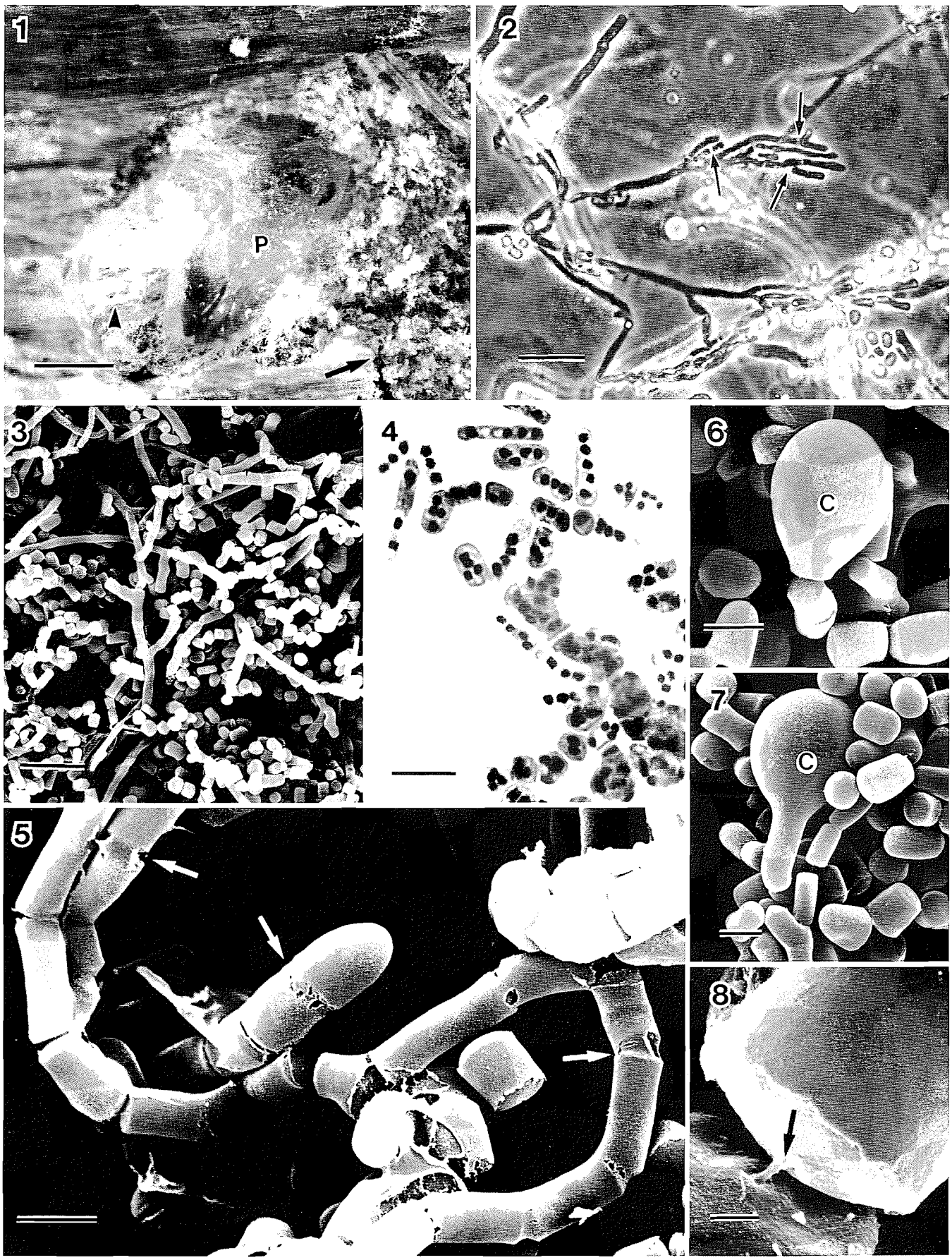
Results

The arthroconidial fungus, UAMH 4919, was found in some pupal chambers of *D. ponderosae* containing live pupae. These chambers were filled with silky white mycelium and the pupa lay on the mycelial mat (Fig. 1). Apparently this fungus preferentially grew in the pupal chambers, since adjacent larval galleries were dominated by colonies of other fungi, such as the *Graphiocladiella* anamorph of *Ceratocystis clavigera* (Robins.-Jeff. & Davids.) Upadhyay. Hyphae bearing clamp connections and basidiomata were not observed either in the natural habitat or in culture.

On agar culture media, the pupal-chamber fungus formed numerous arthroconidia by schizolytic separation of hyphal septa. The septum schizolysis occurred more or less randomly, or sometimes from tip to bottom of fertile hyphae that were either undifferentiated or wider than vegetative hyphae and were often branched (Figs. 2–4). The conidia were dry, hyaline, barrel-shaped or cylindrical, smooth, and mostly single-celled and multinucleate (Fig. 4). When viewed by LM, narrow separation cells appeared between some adjacent cells (Fig. 2, arrows), but SEM revealed that this was caused by incomplete lysis of the hyphal wall (Fig. 5, arrows). Thick-walled chlamydospore-like propagules occurred. They were sessile or occasionally stalked, multinucleate, and separated by septum schizolysis (Figs. 6 and 7). Attachment material of septa often persisted between separating cells (Fig. 8).

The septum of the pupal-chamber fungus was of the dolipore–parenthesome type provided with electron-dense pore plugs at maturity (Fig. 9). Figures 9–13 demonstrate the typical stages in septum modification that occurred during arthroconidiogenesis. The first apparent indication of cell separation was disintegration of the swollen inner edges of the dolipore wall and subsequent occlusion of the dolipore channel as the inner walls of the pore fused (Fig. 10). Subsequently, progressive shrinkage of the fused dolipore wall occurred accompanied by the retraction of the associated parenthesomes and dissolution of the peripheral areas (triangular in longitudinal section) of the cross wall (Fig. 11); this statement is based on the observation of serial sections. The cross wall then split along the median electron-light layer to complete cell separation. Remnants of the dolipore wall (Fig. 12) remained visible until very late stages of, or even after, cell separation. The lateral outer wall overlying the polar cross walls of adjacent cells often persisted between otherwise separated conidia (Fig. 13). All wall layers of the mother cells were incorporated in the conidial wall, and no additional layer developed during conidiogenesis.

In comparison with the pupal-chamber fungus, selected strains of groups 1–4 were examined microscopically (Table 1). All the presumed basidiomycetes (groups 1, 3, and 4) and *P. radiata*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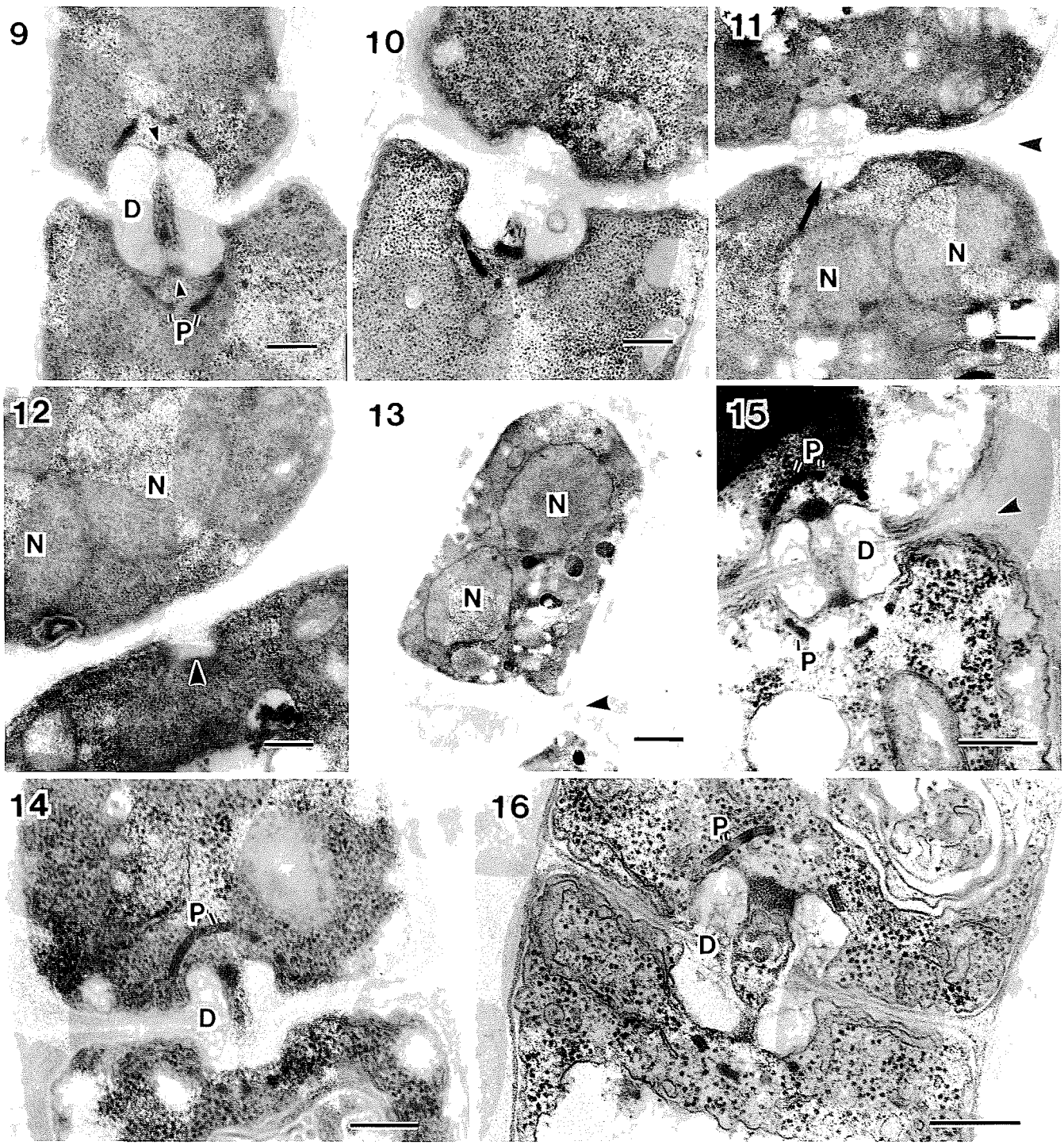
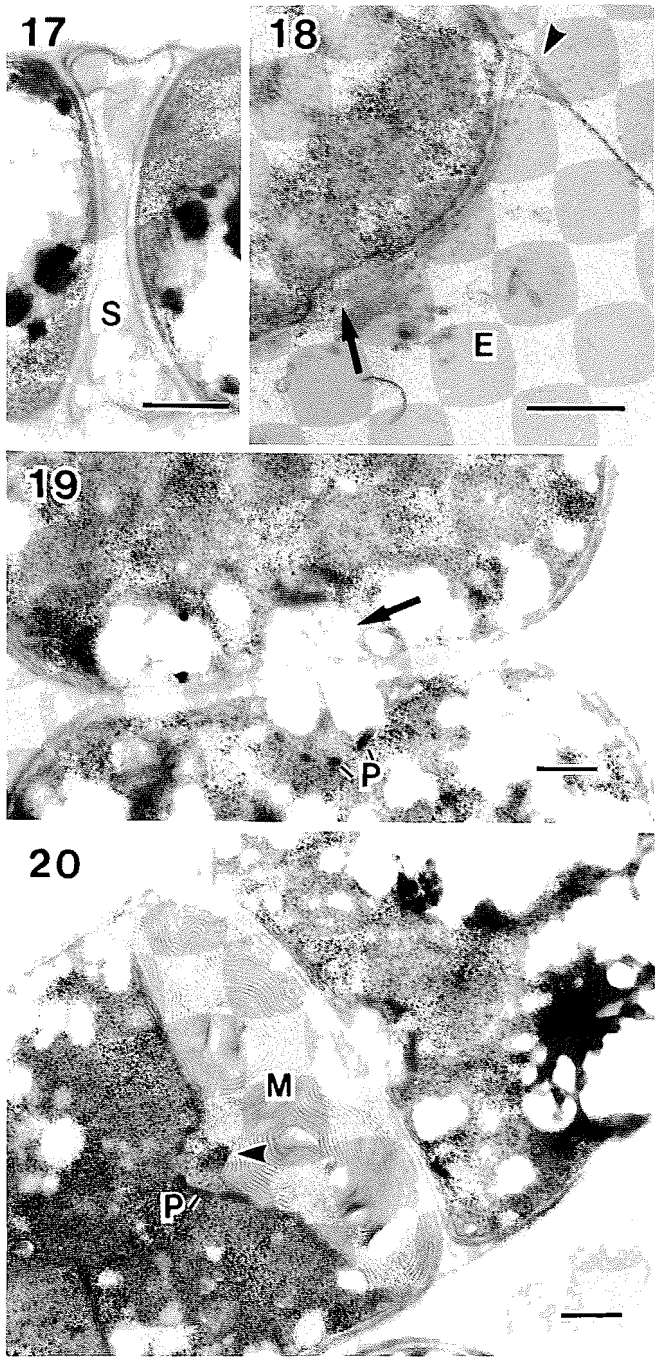
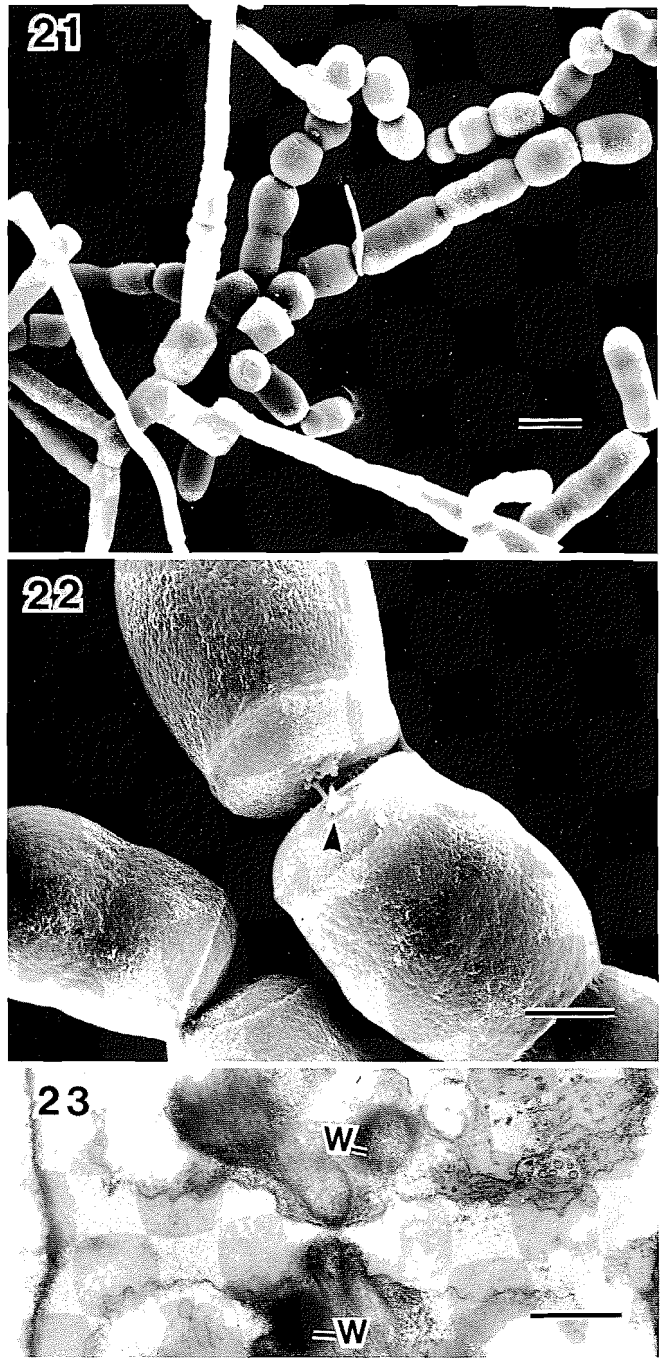


FIGS. 9–16. Transmission electron micrographs of group 1 basidiomycete anamorphs and *Phlebia radiata* (group 2). D, dolipore–parenthesome septum; N, nucleus; P, parenthesome. Scale bars (except Fig. 13) = 0.5 μm. Figs. 9–13. Typical process of septum schizolysis in arthroconidiogenesis by the pupal-chamber fungus (UAMH 4919). Fig. 9. Septal pore plugs (arrowheads). Fig. 10. Occlusion of dolipore channel. Fig. 11. Shrinkage of the dolipore wall (arrow) and splitting of the cross wall (arrowhead). Fig. 12. Remaining dolipore wall just prior to cell separation (arrowhead). Fig. 13. Arthroconidium bearing incompletely lysed outer hyphal wall (arrowhead). Scale bar = 1 μm. Fig. 14. UAMH 448. Fig. 15. UAMH 4259. Cross-wall separation appears to be nearly to the dolipore, but the dolipore–parenthesome complex shows no apparent changes. Fig. 16. Dolipore–parenthesome septum of *P. radiata*.

FIGS. 1–8. Arthroconidial basidiomycete anamorph (UAMH 4919) isolated from a pupal chamber of *Dendroctonus ponderosae*. Fig. 1. Pupal chamber with a pupa (P) lined by a fungal mycelium (arrowhead). The arrow points to an adjoining gallery filled with ambrosial fungi. Scale bar = 2 mm. Figs. 2 and 3. Arthroconidiation on agar medium. Intercellular spaces, as seen by light microscopy in Fig. 2 (arrows), are also demonstrated by SEM in Fig. 5 (arrows). Scale bars = 20 μm. Fig. 4. Multinucleate arthroconidia. Scale bar = 10 μm. Fig. 5. Separating hyphal cells. Arrows point to incompletely lysed hyphal walls. Scale bar = 5 μm. Figs. 6 and 7. Sessile and stalked chlamydospore-like propagules (C) separated by septum schizolysis. Scale bars = 5 μm. Fig. 8. Attachment material (arrow) persisting between separating cells. Scale bar = 0.5 μm.



FIGS. 17–20. Group 3 (Figs. 17–19, UAMH 645) and group 4 (Fig. 20, UAMH 514) basidiomycete anamorphs. E, degenerated cell; M, concentric membranous figure; P, parenthesome; S, separation cell. Fig. 17. Narrow separation cell containing remnants of membranous material. Scale bar = 1 μm. Fig. 18. Late stage of rhexolytic conidial secession. Dolipore wall has degenerated (arrow) but the cross wall including the triangular region (arrowhead) is intact. Scale bar = 0.5 μm. Fig. 19. Schizolytically separating cells with fused dolipore walls (arrow). Scale bar = 0.5 μm. Fig. 20. Early stage of rhexolytic conidial secession showing proliferating membranous figure. The arrowhead points to septal plug material. Scale bar = 0.5 μm.



FIGS. 21–23. *Mauginiella scaettae* (UAMH 4291). Figs. 21 and 22. Schizolytic conidial secession. The arrowhead in Fig. 22 points to septal plug material. Scale bars = 10 μm (Fig. 21) and 3 μm (Fig. 22). Fig. 23. Simple septum provided with Woronin bodies (W). Scale bar = 1 μm.

(group 2) possessed typical dolipore–parenthesome septa (Figs. 14–16, 19, 20). Hyphal cell walls varied with strain in thickness and electron density and were either two- or three-layered. Arthroconidia were invariably dry, smooth, and mostly single-celled. Conidia in groups 1, 3, and 4 contained one to several nuclei. In *P. radiata*, conidia were predominantly uninucleate and rarely binucleate. Dikaryotic hyphae of *P. radiata* did not break up into arthroconidia. Terminal or intercalary chlamydospore-like propagules were produced by most strains.

Arthroconidiogenesis of the group 1 fungi (Table 1) and *P. radiata* was essentially the same as that of the pupal-chamber fungus, except that the dolipore apparatus in UAMH 4259 tended to remain intact until dissolution and splitting of septal cross wall was well advanced (Fig. 15). In UAMH 645

(group 3), conidial secession was predominantly by septum schizolysis. Narrow separation cells were present (Fig. 17), but their occurrence was inconsistent. On the other hand, incomplete wall lysis was frequent and sometimes the dissolution and splitting of septal cross wall failed to occur even after the dolipore apparatus had disintegrated. In such cases, one of the cells separated by the intact cross wall often became empty (Fig. 18) and its lateral walls eventually collapsed. Arthroconidia in the group 4 strain, UAMH 514, dehisced either by septum schizolysis or by rhexolysis; no unique feature was evident in the former mode (Fig. 19), whereas its rhexolytic process was somewhat peculiar with respect to the degenerative process observed in cells subtending incipient conidia. In these cells, multilaminar and concentric proliferation of membranous material developed within the degenerating dolipore and eventually extended across the full length of the cell, forcing the pore plug and parenthesome away from the septum (Fig. 20). This concentric membrane figure, which looked like a vacuole with the LM, finally filled the entire cell before the cell collapsed. These collapsed intervening cells adhered, as stringy wall remnants, to adjacent arthroconidia.

Mauginiella scaettae, when examined by LM or SEM, closely resembled the pupal-chamber fungus in hyphal morphology and in the mode of septum schizolysis (Figs. 21 and 22). However, we confirmed by TEM that its septum was of the simple type provided with Woronin bodies (Fig. 23). Further, unlike the basidiomycete fungi examined here, the conidia of *M. scaettae* were often 1- to 2- (or up to 6-) septate, had a finely wrinkled surface (Fig. 22), and were extremely hydrophobic.

Discussion

Dendroctonus ponderosae, the mountain pine beetle, is probably the most serious enemy of mature pines in western Canada (Safranyik et al. 1974). It is well known that the brood galleries and pupal chambers of this beetle are colonized by yeasts, species of *Ceratocystis* Ellis & Halst. and their anamorphs, and some other conidial fungi (Robinson 1962; Whitney 1971; Sigler et al. 1982; Tsuneda and Hiratsuka 1984; Tsuneda et al. 1986). As for basidiomycetes associated with bark beetles, Whitney et al. (1987) assembled and briefly reviewed the scant literature and described a new basidiomycete, *Entomocorticium dendroctoni* Whitn., Band. & Oberw., which produced abundant basidiospores in the galleries and pupal chambers of the mountain pine bark beetle in lodgepole pine. As far as we are aware, our report is the first one of the occurrence of an arthroconidial basidiomycete occurring in association with living pupae. According to Whitney (1971) and Whitney et al. (1987), the newly formed adults need to feed on the pupal-chamber fungi to complete their maturation. The fungi are then disseminated by the beetle. It is possible that our isolate is one of such fungi.

The septal pore ultrastructure is assumed to be an evolutionarily conserved feature and thus is useful in fungal taxonomy (Moore 1980; Khan and Kimbrough 1982; Bandoni 1984). Particularly the dolipore–parenthesome septum is used as a primary character in defining the higher basidiomycetes (Moore and Marchant 1972). Our study showed that all the fungi listed in Table 1 had typical dolipore–parenthesome septa. Although the pupal-chamber fungus and other group 1 fungi resembled *M. scaettae* in the mode of conidiogenesis, they were clearly differentiated by the septum type. We confirmed that the septum of *M. scaettae* is of the simple type as previously reported by von Arx et al. (1981). The dolipore–parenthesome septum also distinguishes the pupal-chamber and group 1 isolates from some hyphomycetous genera with basidiomycetous affinities, including *Moniliella* Stolk & Dakin, *Trichosporonoides* Haskins & Spencer, and *Hyalodendron* Diddens, each having dolipore septa without parenthesomes. These fungi also show developmental differences, since they produce both blastic and arthric conidia (de Hoog 1979; Martinez 1979; Inglis et al. 1992).

Moore (1977) examined the sequence of dolipore disjunction during arthroconidiogenesis in the coremioid *Antromycopsis* anamorph of *Pleurotus cystidiosus* Miller. Major steps described were (*i*) rupture of the hyphal wall on the circumferential triangular region of the septum, (*ii*) centripetal splitting of the septal cross wall, (*iii*) formation of a new conidial wall beneath the gelatinizing outer wall, and breakdown of the half of the dolipore within the conidium, and (*iv*) separation of the mature conidium. Unlike *Antromycopsis*, none of the fungi examined in this study developed a secondary conidial wall during cell separation, and the breakdown of dolipore apparatus occurred more or less simultaneously on both sides of the septal cross wall.

The pupal-chamber fungus and the group 1 strains (Table 1) possessed the following characteristics: (*i*) hyphae bear no clamp connections, and fertile ones are undifferentiated or wider than vegetative ones; (*ii*) septa are of dolipore–parenthesome type; (*iii*) arthroconidiogenesis is by septum schizolysis; and (*iv*) arthroconidia are dry, hyaline, smooth, barrel-shaped or cylindrical, mostly single-celled, and contain one to several nuclei. The primary mycelium of *P. radiata* (group 2) also shared these characteristics. Sigler and Carmichael (1976) distinguished group 3 by the development of narrow separation cells between maturing arthroconidia, but their occurrence was inconsistent in the strain used in this study. Unlike in groups 1 and 2, rhexolytic conidial secession was common in UAMH 645 (group 3) and predominant in UAMH 514 (group 4), but schizolytic separation of conidia also occurred in both strains. The mechanism controlling the method of conidial secession is unknown. According to Sigler and Carmichael (1976), group 4 is distinctive in that the protoplasm in the fertile hypha becomes condensed in segments separated by vacuoles and then the condensed portions develop a septum at each end to become conidia. In UAMH 514, however, septation of the fertile hypha occurred first and a characteristic membranous structure proliferated in alternate cells that then collapsed to separate conidia.

Tzean and Estey (1991) described *Geotrichopsis mycoparasitica* for an arthroconidial fungus with dolipore–parenthesome septum. Initially found to parasitize some nematode-trapping fungi, the fungus was also shown to be parasitic on a wide variety of fungi (Tzean and Estey 1992). They compared their isolate with representative cultures of several named basidiomycetes including *P. radiata*, placed by Sigler and Carmichael (1976) in their group 2. Two other isolates studied by them (UAMH 448 and 507) had been placed by Sigler and Carmichael in group 1, but Tzean and Estey (1992) considered them to be distinct from their taxon on the basis of macro- and microscopic features and on general proteins and isozymes (unpublished data). Since one of their studied strains (UAMH 448) was also examined by us, we conclude that the pupal-chamber fungus and some other members of group 1 are not conspecific with *G. mycoparasitica*. Investigations are ongoing to determine whether *Geotrichopsis* might be appropriate for disposition of the *Dendroctonus*-associated fungus.

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