Eocronarium muscicola: a basidiomycetous moss parasite exploiting gametophytic transfer cells

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The host–parasite interface in Eocronarium muscicola, Auriculariales sensu lato, was examined histologically for 6 of the 21 reported moss hosts, using light microscopy, scanning electron microscopy, and transmission electron microscopy. A unique mode of fungal biotrophy was encountered in 5 of the 6 mosees analyzed, in which E. muscicola exploits gametophytic host transfer cells concomitant with varying degrees of supplantation of the moss sporophyte. Basidiocarps are restricted in these mosses to postfertilized archegonia, in which they are seen to associate with the sporophyte foot region, where they gain access to the host transfer cell nutritional interface. Basidiocarp ontogeny is presented as it relates to the development of the host–parasite interface. The relationship of E. muscicola to other simple-septate auricularioid taxa and the the Uredinales is discussed.


Introduction

Eocronarium muscicola (Fr.) Fitz., Auriculariales sensu lato, is a small heterobasidiomycete found parasitizing numerous temperate moss genera. The genus was established to accommodate a gelatinous, clavarioid hymenomycete bearing transversely septe metabasidia superficially reminiscent of the telial horn found in the uredinalean genus Cronartium (Atkinson 1902). Stanley (1940) described a thin-walled basidium, carrying the fusion nucleus, as well as basidio- spore germination by the production of secondary basidiospores. Septal ultrastructural studies have revealed a simple septum as in the Uredinales (Khan and Kimbrough 1980) and differing significantly from that found in Auricularia (McLaughlin 1980). Because of the presumed phyllogenetic antiquity of the host group, the presence of thin-walled basidia germinating without dormancy to yield rust-like metabasidia, and the simple septa, E. muscicola occupies a pivotal position in the phylogenies of the lower basidiomycetes proposed by numerous authors (Bandoni 1984; Donk 1972; Hennen and Buirica 1980; Khan and Kimbrough 1982; Leppik 1955; Oberwinkler 1982).

The nutritional mode used by E. muscicola was first described by Fitzpatrick (1918a, 1918b). In Cladonia americanum Brid., Fitzpatrick determined the host–parasite interface to be entirely intracellular and concluded that E. muscicola was restricted to the gametophytic tissues of its host, eventually forming clavate basidiocarps at the apices of moss branches. In rare instances he did note that both the gametophyte and the sporophyte were parasitized, the fungus inhibiting the latter’s development. Ulvinnen (1981) noted that in Fissidens viridulus (Sw.) Warnst. the fungus, in a single instance, parasitized both the gametophyte and the sporophyte. Olive (1948) also collected E. muscicola on the sporophyte of Amblystegium. Aside from these singular observations, subsequent authors have considered E. muscicola to be wholly restricted to the gametophyte and to behave as an intracellular parasite (Bessey 1950; Julich 1982; Khan and Kimbrough 1980, 1982; Stanley 1940).

The present study was initiated to determine whether biotrophy as described in C. americanum (Fitzpatrick 1918a, 1918b) was operative among the other reported moss hosts. Specifically, the host–parasite interface was examined to clarify the relationship between those fungal hyphae comprising the bulbous basidiocarps and the surrounding gametophytic and (or) sporophytic host tissue. Basidiocarp ontogeny is also presented as it relates to the development of the host–parasite interface.

Materials and methods

Six of the 21 reported moss hosts were analyzed histologically (see Table 1) using light microscopy (LM), scanning electron microscopy (SEM), and transmission electron microscopy (TEM). Living Pylaesiella polyantha (Hedw.) Grout (McLaughlin 334, 5 July 1985, host det. J. A. Janssens, MIN) and Haplocladium microphyllum (Hedw.) Broth. (McLaughlin 339, 18 July 1985, host det. J. A. Janssens, MIN), bearing basidiocarps of Eocronarium muscicola, were collected near Dam Lake, Aitkin Co., MN. Infected herbarium specimens of Drepanoelus uncinnatus (Hedw.) Warnst. (Heikkila 81-51; Joensuu, Finland, 8 Aug. 1981, OULU), Fissidens viridulus (Sw.) Wahl. (Särenkoski/Ulvinen; Helsinki, Finland, 28 July 1979, OULU), Pylaesiella polyantha (Hedw.) Grout (Oblenja; Oulunsalo, Finland, 8 Sept. 1982, OULU), Euryhynchium hians (Hedw.) Sande Lac. (Särenkoski 20981/Korhonen 3901; Helsinki, Finland, 20 July

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1981, OULU), and Climacium dendroides (Hedw.) Web. & Mohr. (Koponen 27642; Varsinai-Suomi, Finland, 21 July 1980, OULU) were kindly supplied to the senior author (E.W.A.B.) by Dr. T. Ulvönen (Botanical Museum, University of Oulu, Finland). Vouchers are deposited in MIN.

The living material was processed for LM, SEM, and TEM while the dried specimens were first rehydrated in aqueous 5% KOH and analyzed primarily by LM and SEM. Living F. polyantha and H. microphyllum, bearing E. muscicola at various stages of development, were fixed overnight with 3% glutaraldehyde in 0.1 M sodium cacodylate buffer, pH 7.2 at 4°C, and rinsed in buffer. TEM material was postfixed for 4 h with 1% OsO₄ in the same buffer at room temperature, and en bloc stained overnight in an aqueous solution of 0.5% uranyl acetate at room temperature in the dark. After acetone dehydration the material was embedded in soft Spurr’s resin (Spurr 1969) and thin sectioned on a Reichert Jung Ultracut-E. Serial thin sections were harvested only 2 × 1 mm slot grids (as in Rowley and Moran, 1975) and then stained for 50 min in 5% aqueous uranyl acetate followed by 45 min in lead citrate, and examined with a Hitachi H-600 transmission electron microscope operated at 75 kV. Material for LM, after primary fixation, was dehydrated as above and embedded in glycol methacrylate (Polysciences, Inc., Warrington, PA). Sections were cut at 4–7 μm and stained in toluidine blue at 60°C.

Material for SEM was critical point dried, sputter coated with gold, and examined with a Hitachi S-450 scanning electron microscope operated at 15 kV. The SEM samples, first photographed in their entirety, were then cryofractured to reveal internal structures. Specimens were immersed in liquid propane (−185°C), surrounded by a liquid nitrogen bath, and cryofractured using precooled razor blades. Liquid propane boiled less vigorously than liquid nitrogen at room temperature and so permitted a more accurate orientation of the sample before cryofracture. Cryofractured specimens were recoated with gold and examined with the scanning electron microscope.

The rehydrated herbarium specimens were fixed overnight in 3% glutaraldehyde in a 0.1 M phosphate buffer, pH 7.0, at 4°C, and processed as above for LM or SEM.

Results

In analyzing 6 of the 21 reported moss hosts for Eoconarthrium muscicola (Table 1) we were able to substantiate Fitzpatrick’s (1918a, 1918b) findings in only one of them, C. dendroides. Intracellular biotrophic hyphae were seen to pass from cell to cell (not illustrated) in a manner identical to that described for C. americanum (Fitzpatrick 1918a, 1918b).

The other five moss hosts analyzed display a remarkably different mode of fungal biotrophy, which as far as is known, has not previously been described. In P. polyantha, H. microphyllum, D. uncinitus, F. viridulus, and Eurohynchium hians, E. muscicola is not seen to fruit at the vegetative branch apices of the gametophyte, as in C. dendroides and C. americanum; instead the basidocarp is restricted to determine gametophytic branch apices bearing postfertilized archegonia (Figs. 1, 2, and 3). Nonfertilized archegonia, identified as such by their reduced size and lack of a developing sporophyte, did not bear basidiocarps of E. muscicola (Fig. 2). Sexual, as distinct from vegetative, moss branch apices bearing archegonia are recognized by the occurrence of somewhat modified leaves, perichaetal bracts, which envelope the archegonial region and are collectively termed the perichaetium (Hebart 1977). Acrocarpous mosses (F. viridulus, this study) bear perichaetia at the apices of determinate leafy shoots, while pleurocarpous mosses (P. polyantha, H. microphyllum, D. uncinitus, and Eurohynchium hians) bear perichaetia at the tips of determinate lateral branches. Basidiocarps of E. muscicola appear to be restricted specifically to gametophytic perichaetia bearing postfertilized archegonia in these acrocarpous and pleurocarpous mosses.

When young, postfertilized perichaetia of D. uncinitus, showing no external evidence of infection (Fig. 4), are cryofractured for SEM (Fig. 5), early stages of basidiocarp ontogeny are revealed. The perichaetal bracts encase a single postfertilized archegonium. The neck canal region and the archegonial venter are exposed in near-medial fracture as are the basidiocarp initials situated above the neck canal (Fig. 5). In a later developmental stage the basidiocarp initials have expanded the archegonial neck canal region in D. uncinitus, fully occupying the vaginal pocket (Fig. 7), and emerge as a loose web of fungal hyphae enveloping the apex of the perichaetium (Fig. 6).

The relationship between the developing sporophyte in the mosses and the basidiocarp initials of E. muscicola shows a certain amount of variability. In D. uncinitus (Figs. 4–7), F. viridulus, and Eurohynchium hians (the latter two not illustrated) the sporophytic generation is arrested early.
in its development by E. muscicola. Rarely does the sporophyte develop beyond the apex of the perichaetium. Pyilaesiella polyantha and H. microphyllum differ in that the sporophyte does develop beyond the perichaetial apex but is then progressively deterred from further growth (Figs. 1–3 and 8–10). In young nonsporulating basidocarps of E. muscicola the sporophyte is encased within the developing fungal fruit body (Fig. 2), and even in mature fruit bodies the arrested sporophyte may remain encased (Fig. 3). Thus, macroscopically the sporophyte—fungus associations are cryptic in D. uncinatus, F. viridulus, and Eurhynchium hians, unless examined in the earliest stages of development, while in P. polyantha and H. microphyllum the sporophyte often persists to varying degrees during the establishment of the fungal fruit body.

When H. microphyllum bearing an arrested sporophyte is examined with LM (Fig. 8), a necrotrophic association is revealed in which fungal hyphae ramify and disrupt the developing sporophyte. The sporophyte, having just emerged from the surrounding perichaetial bracts, has not yet ruptured the calyptra. Figures 9–11 illustrate H. microphyllum at a later developmental stage, in which the sporophyte is not completely ensheathed by fungal hyphae and protrudes beyond the perichaetial bracts. A near-medial fracture reveals fungal hyphae within the central core of the sporophyte (Fig. 10).

Hyphae of basidocarp initials of E. muscicola infiltrate the sporophytic tissue and eventually supplant it completely so that very little, if any, remains at maturity (Figs. 11 and 12). However, as mentioned before, remnants of the sporophyte often may persist in H. microphyllum and P. polyantha. A traverse fracture through the basal region of a mature basidocarp reveals a central core of gelatinized hyphae, constituting the central axis of the fruit body, surrounded by perichaetial bracts, some of which have been penetrated by fungal hyphae, and enveloped in a loose external hyphal felt (Fig. 11).

The mature basidocarp sits in a pocket of gametophytic tissue termed the vaginula (Fig. 12), which remains chlorophyllous and apparently unaffected by the presence of the biotroph. In uninfected mosses the sporophyte foot is situated within the vaginula (Hebant 1977). In this particular longitudinal section of P. polyantha (Fig. 12) no remnants of the sporophyte are discernable, but in other sections of the same moss they were (not illustrated). In no instance were hyphae associated with the bulbous fruit-body base seen to penetrate adjacent host cells in P. polyantha, H. microphyllum, D. uncinatus, F. viridulus, and Eurhynchium hians, as has been reported and confirmed for the Climacium species. Instead, interfacial phenomena reported as commonly occurring in uninfected gametophyte-sporophyte interactions are encountered.

The fruit-body base of E. muscicola is surrounded by host gametophytic transfer cells (Figs. 12–17). The transfer cells are characterized by secondary wall appositions forming invaginations along the inner wall adjacent to the biotrophic hyphae (Figs. 13, 14, and 17). The far wall of the host transfer cells bears no invaginations (Fig. 13). The presence of nuclei and nucleoli in the transfer cells attests to their viability (Fig. 14). Interestingly, where fungal hyphae deviate intercellularly from the main axis of the fruit body, host transfer cells are seen to differentiate (Fig. 13). The secondary wall of the transfer cell can clearly be distinguished from the primary wall (Figs. 16 and 17) and the invaginations of the former often diverge from the vaginular pocket into the loose gametophytic tissue. Scale, 500 μm.

Figs. 1 and 2. Haplocodiurn microphyllum with developing basidocarps of Eacronortium muscicola associated with postfertilized perichaetia bearing arrested sporophytes (sp). Note the diminished size of unfertilized perichaetia (white arrowhead) in Fig. 2. Scales, 1 mm. Figs. 3. Pyilaesiella polyantha with mature basidocarp of E. muscicola encasing an arrested sporophyte (sp). Haplocodiurn microphyllum and P. polyantha tend to retain the sporophyte to varying degrees during the biotrophy, while in the other mosses analyzed it is rapidly displaced by the fungus. Scale, 1 mm. Figs. 4–7. SEM of Drepanocladus uncinatus and E. muscicola. Figs. 4 and 5. Surface view and cryofracture of the same specimen. Fig. 4. Young postfertilized perichaetium showing no external evidence of infection. Scale, 250 μm. Fig. 5. Cryofracture revealing the vaginula (v), perichaetial bracts (p), and developing basidocarp (bc) situated above the archegonial neck canal region (n). Scale, 250 μm. Figs. 6 and 7. Surface view and cryofracture of the same specimen at a later stage of development. Fig. 6. Basidocarpic initials emerging from the perichaetial bracts (arrowhead) in loose hyphal weth. Scale, 500 μm. Fig. 7. Cryofracture revealing the expanded archegonium (arrowhead) in which no trace of the sporophyte is discernable, having been completely supplanted by biotrophic hyphae. In no instance are hyphae seen to diverge from the vaginular pocket into the loose gametophytic tissue. Scale, 500 μm.

Figs. 8–11. Haplocodiurn microphyllum with Eacronortium muscicola. Fig. 8. LM illustrating the necrotrophic association in which hyphae of E. muscicola ramify and disrupt the developing seta (s) of the host sporophyte. This necrotrophic association ceases when hyphae encounter gametophytic tissue. The seta (s) has not emerged from the calyptra (c). This is a similar developmental stage as that illustrated in Fig. 2. Scale, 250 μm. Figs. 9 and 10. SEM of the surface view and cryofracture of the same specimen. Fig. 9. The sporophyte (arrow), having emerged from the surrounding perichaetial bracts, is arrested and encased in basidocarpic hyphae. Scale, 250 μm. Fig. 10. A near-medial fracture reveals fungal hyphae within the central core of the seta and occupying the vaginular pocket. Scale, 250 μm. Fig. 11. A transverse fracture through the basal region of a mature basidocarp showing a central core of thick-walled, gelatinized hyphae comprising the central axis of the fruit body (bc), surrounded by perichaetial bracts (p), some of which have been penetrated by fungal hyphae (arrow), and enveloped in a loose external hyphal felt (eh). Scale, 50 μm.

Figs. 12 and 13. Pyilaesiella polyantha with Eacronortium muscicola. Fig. 12. LM of a medial longitudinal section through a mature basidocarp. The fruit-body base is situated within the vaginula (VA), which remains chlorophyllous. In unfertilized mosses the sporophyte foot occupies this region. Remnants of the sporophyte were detected in adjoining sections (not illustrated). The fruit-body base is surrounded by gametophytic host transfer cells (arrowheads). Scale, 250 μm. Fig. 13. LM on a longitudinal section illustrating the host—parasite interface. Note that the secondary wall appositions (arrows), characterizing transfer cells, are differentiated only along the abutting host wall. Where fungal hyphae deviate laterally from the main axis of the fruit body, transfer cells are differentiated (open arrow). Scale, 50 μm. Fig. 14. LM of Haplocodiurn microphyllum and E. muscicola. Host—parasite interface illustrating secondary wall appositions (solid arrows) along the host wall directly abutting fungal hyphae. Note host cell nucleus and nucleolus (open arrow). Scale, 25 μm. Fig. 15. SEM of Pyilaesiella polyantha and E. muscicola cryofracture revealing secondary wall appositions, characterizing gametophytic transfer cells. Note some wall protrusions are branched (arrowhead). Scale, 5 μm. Figs. 16 and 17. TEM of Haplocodiurn microphyllum and E. muscicola. Fig. 16. The fungus — gametophytic host nutritional interface. The secondary (2) wall appositions, characterizing the host transfer cell, can clearly be distinguished from the primary (1) wall. Note the plasma membrane (arrow) continuity over the secondary wall appositions. Scale, 0.5 μm. Fig. 17. Note the labyrinthine nature of the secondary wall appositions. Scale, 1.5 μm. Host (H) and fungus (F).
anastomose to form labyrinths (Fig. 17) or dichotomous branches (Fig. 15). The host plasma membrane forms a continuum around the wall appositions (Fig. 16). The host transfer cells do not appear to form a distinct band or collar around the fruit-body base (Fig. 12), as has been reported in uninoculated gametophyte—sporophyte associations (Wiencke and Schultz 1975), but instead are randomly distributed. In the host, hydroids, water-conducting elements, have been observed subtending the fruit-body base (not illustrated).

**Discussion**

_Eocronartium muscicola_ establishes a unique biotrophic relationship, characterized by a host transfer cell nutritional interface, with a diverse assemblage of moss hosts. Fungal hyphae are seen to attack and eventually supplant entirely the developing sporophyte generation in the mosses analyzed in this study, with the sole exception of _C. dendroides_. Interestingly, this necrotrophic association ceases when host gametophytic tissue is encountered. If the mature basidioecarp—moss association is analyzed histologically without first studying the earlier developmental stages, the disintegration of the moss sporophyte and, hence, the nature of the fertilized perichaetial region as the site of fungal sporulation may remain undetected.

Transfer cells are induced to differentiate in response to fertilization in many bryophytes (Hebant 1975; Kelly 1969; Wiencke and Schultz 1975). Transfer cells may exist in both the gametophyte and the sporophyte (Eyme and Suire 1967) or they may be present solely on the sporophytic (Maire 1967) or gametophytic (Gunning and Pate 1969) side of the interface. Since no plasmodesmal connection links the two generations (Hebant 1977), the increased surface-to-volume ratios afforded by wall ingrowths greatly increase the surface area of the plasma membrane and, therefore, augment transport of solutes between generations. Histochemical studies have shown that transfer cells are the site of intense enzymatic activities, especially of phosphatases and respiratory enzymes (Hebant and Suire 1974). High mitochondrial populations also characterize these zones (Hebant 1977). In certain Polytrichales (Maire and Maire 1972; Hebant 1975) extensive systems of endoplasmic reticulum have been reported. Specialized ER arrays have similarly been observed in various other cell types implicated in transport phenomena (Hebant 1977). Although structurally well characterized, bryophyllous transfer cells are less well understood physiologically. Nevertheless, the gametophyte—sporophyte interface must represent a demanding nutritional sink, at least during the early stages of sporophyte development. According to Wiencke and Schultz (1975) the transport of nutrients to the sporophyte ceases after two-thirds of its development. Such a nutritional sink offers a unique niche for a biotrophic fungus capable of securing nutrients without undue damage to the host. Occupying the position of the sporophyte enables the biotroph to have direct access to the gametophytic transfer cell apparatus.

Amplification of interfacial membrane systems is not restricted to the bryophytes, having been well documented in a wide variety of anatomical situations within the higher plants (Gunning and Pate 1969; Browning and Gunning 1977). Transfer cells have also been recorded from interfaces involving dissimilar organisms including examples of basidiomycetous fungi involved in higher plant transfer cell associations. Monotropical ectomycorrhizal associations apparently involve the inducement by the mycobiont of localized host transfer cells (Duddridge and Read 1982; Robertson and Robertson 1982) in which host wall appositions form in response to determinate hyphal protrusions into adjacent epidermal cells. Ashford and Allaway (1982) have found, in _Pisonia grandis_ R. Br., that a wall labyrinth is differentiated along host walls directly abutting sheathing ectomycorrhizal hyphae. The ectomycorrhizal association is unusual in that, in place of the Hartig net, fungal-induced host transfer cells serve a similar function to augment the surface-to-volume ratio (Allaway et al. 1985). Transfer cells have also been induced in vitro between ectomycorrhizal associates that in vivo do not normally induce such cells (Duddridge and Read 1984). Transfer cells have also been reported in the _Alnus crispa_—_Alpova diplophloea_ ectomycorrhizal association (Massicotte et al. 1986).

Roth (1969) has demonstrated that a conducting strand linking the archegonium with the central axial strand of the gametophyte is established only by the presence of a developing embryo and that nonfertilized archegonia degenerate by the failure to establish this vascular connection. Similar findings have been recorded for other mosses (Hebant 1977). _Eocronartium muscicola_ seems to establish basidiocarpic initials only in postfertilized archegonial regions, i.e., those bearing developing embryos. This fact suggests that these regions, in contrast to nonfertilized archegonia, apparently provide the necessary vascular connection to establish the perichaetium as a nutritional sink, capable of supporting a sporulating fungal fruit body.

Is _E. muscicola_ actually inducing the transfer cells so as to facilitate nutrient uptake or is the fungus simply utilizing preformed transfer cells? It seems that transfer cells, for the most part, are exploited as preformed structures, under the inducement of the developing sporophyte prior to its supplantation. The mosses _H. microphyllum_ and _P. polyantha_, which retain sporophytes for longer periods, tend to display a greater number of transfer cells than do those mosses in which sporophytes are rapidly displaced by the developing fungus, i.e., _D. uncinatus, F. viridulus_, and _Eurhynchium hians_. Clearly, a nutritional advantage is gained in those associations where _E. muscicola_ is capable of a prolonged biotrophy without rapid degeneration of the sporophyte. _Eocronartium muscicola_, however, appears to possess a limited capacity for inducing host transfer cells. When basidiocarpic hyphae penetrate between cells of the host gametophyte, transfer cells are seen to differentiate.

Growing apices also are believed to represent nutrient sinks to which photosynthates are transported (Richardson 1981). _Climaciun_ species rarely produce sporophytes (Fitzpatrick 1918a), which may explain the association of _E. muscicola_ as an intracellular fungal parasite in branch apices of _C. americanum_ and _C. dendroides_. Unfortunately, Fitzpatrick (1918a) concentrated his histological analysis primarily on _C. americanum_ and, thus, erroneously concluded that _E. muscicola_ behaved solely as an intracellular parasite among all of its moss hosts. The present study clarifies the heterogeneity observed in the nutritional modes among the various hosts. _Eocronartium muscicola_ may represent a diverse assemblage of physiologic races capable of different degrees of fungal biotrophy, and (or) genetic differences in the hosts may account for the diversity of biotrophic responses. The fungus is capable of (i) a mild biotrophy, as in _H. microphyllum_ and _P. polyantha_, in which the sporophyte persists and hence a greater number of transfer cells may be exploited or (ii) a more aggres-
sive biotrophy, where the host sporophyte is arrested early in its development, as in *D. uncinctus*, *Eurynchium hians*, and *F. viridulus*, or (iii), where sporophytes are infrequently produced, as in *Climacium* species, exploitation of another available nutritional sink, the gametophytic branch apices, occurs.

Despite Fitzpatrick's (1918a) detailed efforts to elucidate the life cycle of *E. muscicola*, including basidiospore inoculation on a wide variety of susceptible mosses, in no instance was successful infection realized. Suspecting an earlier stage in the life cycle of the host to be susceptible, Fitzpatrick (1918a) cultured protonema, derived from *Brachythecium oxycladon* (Br.) Jaeg. & Sauerb., with germinating basidiospores, again without success. This latter failure, however, may have been because the dual cultures were retained for only 1 week. The current study did not attempt to examine the life cycle of *E. muscicola*. Presently, therefore, the ecology and manner by which the fungus becomes established remain unknown. However, numerous moss archegonia produce a simple sugar acting as a sperm attractant (Machlis and Rawitscher-Kunkel 1967). Germinating basidiospores on the moss surface may grow unidirectionally towards the archegonium following a sugar gradient through the water film, although this has not been substantiated.

*Eocoronarium muscicola* is taxonomically related to species of *Jola* (Gaumann 1922; Khan and Kimbrough 1980, 1982; Lowy 1971; Martin 1939; Oberwinkler and Bandoni 1982, 1984; Stanley 1940), also members of the simple-septate Auriculariales *sensu lato* parasitizing mosses. *Jola* fructifications, however, are restricted to the apex of the sporophytes of the tropical mosses it parasites. It also likely exploits transfer cells but indirectly via the sporophyte, which serves as a nutritional bridge, unlike *E. muscicola*, in which transfer cells are exploited directly by the supplantation of the host sporophyte. Both *Eocoronarium* and *Jola* parasitize moss sporophytes, the latter being restricted to the capsule while the former supplanting it to varying degrees.

The simple-septate auricularioid taxa encompass many nutri
tional modes ranging from biotrophy to saprotrophy. *Eocoro
narium muscicola*, unlike the rusts, does not produce haustoria but rather makes use of gametophytic nutritional sinks often via host transfer cell exploitation. The host-
parasite interface in *Jola* has not been analyzed, but it is assumed to be restricted to diploid tissue (Gaumann 1922). *Herbopasidium* and *Platyacarpa*, auricularioid fern parasites, produce elongate, coiled haustoria (Oberwinkler and Bandoni 1984). Haustoria within the Pucciniaceae, Uredinales, show a trend towards an economy of surface area, with large, digitate and lobed haustoria in primitive rusts parasitizing ferns to smaller haustoria in more advanced groups (Moss 1926). The auricularioid fern parasites show some haustorial similarity with the rusts, but the phylogenetic significance of the host—parasite interface in *E. muscicola* remains unclear. It appears to be strikingly different from the host—parasite interface in the uruedinal and auricularioid fern parasites. It may reflect the distinctive nature of the bryophytic host group. The nonhaustorial intracellular hyphae of *E. muscicola* in *Climacium* species are comparable with monokaryotic hyphae in some rusts (Harder and Chong 1984), but they are dikaryotic in *E. muscicola*.

*Eocoronarium* and *Jola* have been proposed as extant representat
tives of the ancestral complex postulated to have given rise to the Uredinales (Hennan and Buritica 1980; Khan and Kimbrough 1980, 1982; Oberwinkler 1982). Hennan and Buritica (1980) have suggested that simple "autoecious aurici
ularioid rusts," parasitic on mosses and ferns (*Eocoronarium*, *Jola*, *Herbopasidium*, and *Platyacarpa*), represent archaic rust lineages with unexpanded life cycles, having never acquired the auxiliary spore states characteristic of the primitive hetero-
macrocytic fern—fruits. Julich (1982) has even established the *Eocoronariaceae* in the Uredinales to accommodate *E. muscicola*; however, this proposal has been criticized (Bandoni 1984). The authors are inclined to agree with Oberwinkler and Bandoni (1982), who suggest the Cystobasidiaceae, Auriculariales *sensu lato*, as a temporary repository for simple-septate auricularioid taxa until a time when sufficient evidence has been accumulated to unite or separate these organisms into a septate order or orders distinct from the Auriculariales *sensu stricto*. Towards this end the authors are currently engaged in an ultrastructural analysis of basidial development and the associated nuclear cycles to characterize further the simple-septate auricularioid taxa.

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