Entomocorticium dendroctoni gen. et sp. nov. (Basidiomycotina), a possible nutritional symbiote of the mountain pine beetle in lodgepole pine in British Columbia

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A new basidiomycete, ***Entomocorticium dendroctoni*** Whitn., Band. & Oberw., gen. et sp. nov., is described and illustrated. This cryptic fungus intermingles with blue stain fungi and produces abundant essentially sessile basidiospores in the galleries and pupal chambers of the mountain pine bark beetle (*Dendroctonus ponderosae* Hopkins Coleoptera: Scolytidae) in lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.). The insect apparently disseminates the fungus. Experimentally, young partially insectary reared adult beetles fed *E. dendroctoni* produced 19% more eggs than beetles fed the blue stain fungi.

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Un nouveau basidiomycète, ***Entomocorticium dendroctoni*** Whitn., Band. & Oberw., gen. et sp. nov., est décrit. Ce champignon cryptique se trouve en compagnie de champignons causant le bleuissement et produit en abondance des basidiospores sessiles dans les galeries et les loges nymphales du dendroctone du pin ponderosa (*Dendroctonus ponderosae* Hopkins Coleoptera: Scolytidae) dans le pin tordu latifolié (*Pinus contorta* Dougl. var. *latifolia* Engelm.). L'insecte semble disséminer le champignon. De jeunes dendroctones adultes, élevés partiellement dans le laboratoire, et auxquels on a donné *E. dendroctoni* en nourriture ont produit 19% de plus d'oeufs que les dendroctones ayant reçu les champignons responsables du bleuissement.

Introduction

It is well documented that bark beetles carry microorganisms into their host trees at the time of penetration. Most notable are the ascomycetous and hyphomycetous blue stain fungi (Francke-Grosmann 1967). However, nonstaining fungal associates have also been reported (see references in Whitney, 1982, and Sigler *et al.*, 1982). Many of these are also ascomycetes and hyphomycetes, but some are basidiomycetes.

One of us (H.S.W.) recently found a cryptic resupinate basidiomycete producing abundant spores (ambrosia) in pupal chambers and on the walls of larval galleries in mountain pine beetle (*Dendroctonus ponderosae* Hopkins) broods on lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) in British Columbia (Figs. 2–4). The scant literature on basidiomycetes associated with bark beetles is assembled for the first time and briefly reviewed, and the new fungus is described and named. Some phylogenetic relationships are discussed, and preliminary observations are presented on the possible role of this fungus as a nutritional symbiote of the mountain pine beetle.

The earliest reported basidiomycete closely associated with bark beetle brood development was tentatively identified as *Dacrymyces* Nees : Fr. (Bramble and Holst 1935). In 1939, *Gloeocystidium ipidophilum* Siemasko was described as new from galleries of *Ips typographus* L. in Poland (Siemaszko 1939). A *Sebacina*-like basidiomycete was associated with pupal chambers of *Ips avulsus* (Eichoff) (Moser and Roton 1971). An undescribed basidiomycete, SJB 122 from *Dendroctonus frontalis* Zimmermann, was the first basidiomycete found in a scolytid mycangium (Barras and Perry 1972; Happ *et al.* 1976). A similar fungus was reported in the mycangium and throughout the habitat of *D. brevicomis* Lec. (Whitney and Cobb 1972; Paine and Birch 1983). *Heterobasidion annosum* (Fr.) Bref. is the only other known basidiomycete intimately associated with developing broods of scolytids (Bakshi 1952; Himes and Skelly 1972). Other reported relationships between bark beetles and basidiomycetes are *H. annosum* as a possible pathogen of *D. valens* Lec. and *Ips paraconfusus* Lanier (Hunt and Cobb 1982), the sporophore of *Phaeolus schweinitzii* (Fr.) Pat. as an hibernation niche for *Trypodendron rufitarsus* (Kirby) (French and Roeper 1972), *Cryptoporus volvatus* (Peck) Shear likely vectored by *D. pseudotsugae* Hopk. (Borden and McClaren 1970; Castello *et al.* 1976; Harrington *et al.* 1981), *Tulasnella* sp. as a primary ambrosial fungus (Batra 1972), and several basidiomycetes disrupting bark beetle brood development by competing with blue stain fungi in colonization of fresh logs of Norway spruce (Dowding 1973). Additionally, the basidiomycetes (*H. annosum, Armillaria mellea* (Vahl : Fr.) Karst. and *Cronartium ribicola* Fisch.) are associated with bark beetles because they cause diseases believed to predispose host trees to beetle attack (Alexander *et al.* 1980; Miller and Partridge 1974; Kulhavey *et al.* 1984). Finally, the basidiomycetes *Cryptoporus volvatus, Peniophora gigantea* (Fr.) Massee, *Fomes pinicola* (Sw. : Fr.) Cke., *Phellinus weirii* (Murr.) Gilbertson, and *Phellinus pini* (Thore : Fr.) Pilat were found in studies of fungal colonization and deterioration of tree stems, stumps, and roots attacked by scolytid beetles (Hopkins 1901; Harrington 1980; Hunt and Cobb 1982; Kulhavy *et al.* 1984;

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Vite and Rudinsky 1962).

The symbiotic role of basidiomycetes, other than SJB 122, that are intimately associated with bark beetles is largely unknown. SJB 122, reported only from the mycangium of the southern pine beetle, may, if it colonized the host tree as well as the mycangium, enhance insect reproduction and growth by lowering the C/N ratio in the beetles' food (Hodges 1968; Barras and Hodges 1969; Bridges 1983). This fungus may also produce volatile compounds that affect beetle behavior (Brand and Barras 1977). The mycangial basidiomycete of the western pine beetle reduced translocation in ponderosa pine seedlings (Paine 1984).

Methods

Pure cultures of *Entomocorticium dendroctoni* were made by streaking basidiospores onto YM/10 agar (2% yeast extract − malt extract agar (YM) diluted to 10 times its volume with 2% water agar) and transferring germinating basidiospores into culture tubes. Hyphal-tip cultures on YM were made from the advancing margin of mycelium growing from small pieces of basidiocarp teased apart on YM/10 agar. For growth-rate studies on various commercially available culture media and determination of an optimum growing temperature, 4 mm diameter discs, cut with a cork borer from the advancing margin of a YM/10 colony, were transferred, mycelium side down, to the center of three replicate 9-cm culture dishes containing uniform aliquots of test media. The plates were incubated upside down in loosely closed plastic bags in the dark. Daily growth was measured by taking the average of the longest and shortest diameter of an expanding colony. Incubation temperatures were 10, 15, 20, 24, and 27, all ±1°C.

Sporogenous cells of *E. dendroctoni* were examined by TEM, using methods described by Oberwinkler and Bandoni (1982).

Bark beetles were partially insectary reared, stored, sexed, and caged onto fresh pine bolts as described by Whitney and Spanier (1982). Field-infested bolts with advanced mountain pine beetle brood from Riske Creek, B.C., were used to obtain fungus-laden pupal chambers (Fig. 3) for studies of maturation feeding. Fresh lodgepole pine bolts, also from Riske Creek, were handled and stored as previously described (Whitney and Spanier 1982). For bioassay of reproduction, pairs of beetles caged onto bolts were incubated in a shadehouse in Victoria, B.C., in August 1978 (mean daily temperature 16.9°C). Twenty-one days after males were introduced to previously established females, the bolts were peeled and measurements made of gallery length and the number of eggs and larvae (Table 1). For bioassay of fungi as possible nutritional factors in the mountain pine beetle's diet, three sets of vials were prepared, one with *E. dendroctoni* basidiospores, one with conidiospores of either or both of the mountain pine beetle blue stain fungi, and one with uncolonized fresh phloem.

TABLE 1. Egg production of adult mountain pine beetle fed *E. dendroctoni* or blue stain fungi for 15 days

		Total no. of eggs laid[a]		
Replicate	Gallery	*E. dendroctoni*[b]	Blue stain fungi[b]	Control[c]
1	1	117	121	115
	2	74	117	108
	3	94	82	113
2	1	127	135	124
	2	131	—	116
	3	—	52	198
3	1	151	99	129
	2	110	106	113
	3	113	49	—
	4	143	—	—
Mean[d]		117.8	95.1	127.0
(Standard error)		(23.89)	(31.69)	(29.45)

[a]At 21 days after introduction of males.
[b]For amount fed see text.
[c]No fungus supplement, beetles fed fresh phloem.
[d]Differences significant (*t*-test) at 99% except 95% between *E. dendroctoni* and control.

Taxonomy

Entomocorticium Whitn., Band. & Oberw. gen. nov.

Basidiocarpa subcorticalis, resupinata, obducens parietes intra larvarum cunicula et puparum cubicula quibusdam scolytidis, membranacea, margine byssoideo, habente fila inconspicua ac radiantia. Superficies hymenii plana et alba vel bubalina. Systema hyphale monomiticum. Hyphae hyalinae, cum fibulis, semper distinctae. Hymenium initio cystidiis abundanter incrustatis, postea spissescens paucis vel nullis cystidiis. Basidia suburniformia vel irregulatum clavata, (1)−4−(6)-spora. Basidiosporae symmetrice per sterigmata brevia et lata portatae, non eiectae, subcylindricae vel ellipsoidae vel subglobosae, ad affixionem truncatae, distaliter rotundatae, hyalinae; muris levibus, crassis, neque amyloideis, neque cyanophilis.

SPECIES TYPICA: *Entomocorticium dendroctoni* Whitn., Band. & Oberw.

ETYMOLOGIA: Ento, insect; corticium, name of a related fungus.

Basidiocarp subcortical, resupinate, lining the walls of larval galleries and pupal chambers of bark beetles, membranaceous, the margin byssoid and with inconspicuous radiating strands. Hymenial surface even, white to buff. Hyphal system monomitic. Hyphae hyaline, with clamps, remaining distinct. Hymenium at first with abundant smooth or incrusted cystidia, later thickening and with few or no cystidia. Basidia suburniform to irregularly clavate, (1)−4−(6)-spored. Basidiospores borne symmetrically on short, broad sterigmata, not abstricted, subcylindric to ellipsoid or subglobose, truncate at the attachment, rounded distally, hyaline, the walls smooth, thick, inamyloid, acyanophilous.

TYPE SPECIES: *Entomocorticium dendroctoni* Whitn., Band. & Oberw.

Entomocorticium dendroctoni Whitney, sp. nov.

Figs. 1−13

Basidiocarpa corticioidea, margine byssoideo, habente fila radiantia, quae plerumque ex minus quam 10 hyphis adhaerentibus et fibulatis componuntur. Basidia et cystidia aut exoriuntur directe ex subiculo aut elevantur ramis brevibus et erectis. Hymenium leve, effusum, initio ad crassitiem 45−50 μm, cystidiis abundantibus, postea usque ad crassitiem circa 500 μm, paucis vel nullis cystidiis in superficie, album vel cremeum vel bubalinum (Pinkish Buff, Light Buff, or Olive Buff (Ridgway 1912)). Hyphae 3−5(−6) μm, muris tenuibus vel crassiusculis, semper distinctae, cum fibulis ad omnia septa, ramis inter fibulas exorientibus. Cystidia 22−60 × 5−10 μm, initio levia et supra crassitunicata, saepe asperescentia tum incrustata, infra incrustationem tenuitunicata et collabentia; pars incrustata lanceolata vel ventricosa vel irregularis, saepe infra zonam incrustatum acute flexa. Basidia 24−27(−31) × 5.5−6.5 μm, clavata vel suburniformia, interdum irregularia, saepius secundarie septata, collabentia post sporarum procreationem, (1)−4−(6)-spora, sporis

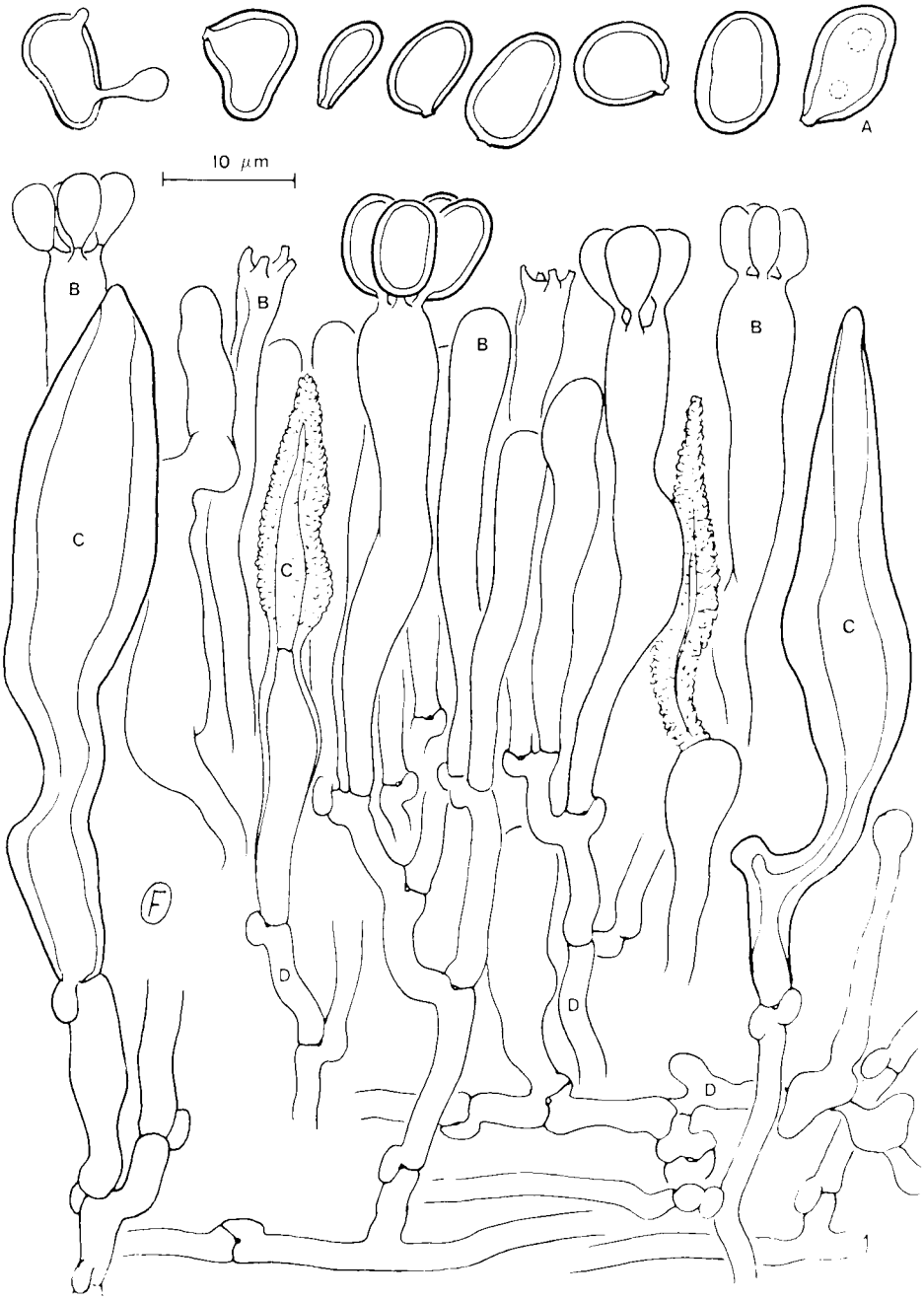

FIG. 1. Drawing of a young fructification of *Entomocorticium dendroctoni*. (A) Variation in size and shape of mature thick-walled basidiospores, one germinating. (B) Development of basidia and basidiospores. (C) Cystidia. (D) Subhymenial hyphae with abundant clamp connections.

symmetrice per sterigmata brevia et lata portatis, non eiectis. Basidiosporae in hymenio accumulantes, sporis singulatim $(7.5-)8-10(-12) \times 4.6$ μm, plerumque subcylindricae, saepe prope medium subattenuatae, interdum late ellipsoidae vel subglobosae et $8-10.5 \times 7.5-10$ μm, affixione truncata, levibus, crassis, apparenter bistratis, neque amyloideis, neque cyanophilis.

HABITAT: Nascitur in puparum cubiculis et in larvarum cuniculis *Dendroctoni ponderosae* Hopkins in *Pinus contorta Dougl.* var. *latifolia* Engelm. DAVFP 23157 Typus.

Basidiocarp primordia at first consisting of an extremely thin, adherent, whitish, byssoid layer and delicate readiating strands, these mostly composed of less than 10 closely adherent, clamped hyphae that branch infrequently, the branches recurving and adherent, single large crystalline deposits at frequent intervals on the strands. Scattered clusters of basidia and cystidia develop, arising either directly on the subicular hyphae or elevated on erect hyphae arising from the subiculum, the hymenium spreading, becoming continuous (Fig. 1), the initial hymenial layer about $45-50$ μm thick, with abundant cystidia, the extremely thin underlying parallel layer of hyphae inconspicuous except at margins and in the initial stages of basidiocarp development, the hymenium thickening, the basidiocarp eventually layered and successive hymenia with few or no cystidia, the total thickness eventually up to ca. 500 μm, white to pale cream or buff (Pinkish Buff, Light Buff,

FIGS. 2–3. Habitat of *Entomocorticium dendroctoni*. Fig. 2. Near the start of mountain pine beetle egg galleries (arrows), suggesting a vector relationship with the beetle. ×0.25. Fig. 3. In pupal chambers, pupae removed. ×0.66.

or Olive Buff (Ridgway 1912)), the surface smooth, separating readily from the substratum. Hyphae 3–5(–6) μm, the walls thin to slightly thickened, remaining distinct, with a clamp at each septum, branches originating between clamps. Cystidia (Fig. 1) 22–60 × 5–10 μm, smooth, thick-walled above, mostly becoming incrusted, thin-walled and sometimes collapsing below the incrustation, incrusted portion lanceolate to ventricose or irregular, often sharply bent basally, especially in those formed initially. Basidia (Fig. 1) 24–27(–31) × 5.5–6.6 μm, clavate or suburniform, often irregular, frequently secondarily septate, collapsing after spore production (often while the spores are still attached), mostly 4-spored, a few with 1, 2, or 6 spores, these born symmetrically on short, broad sterigmata. Basidiospores accumulating to form a fragile crust on the hymenium (Figs. 2–4), the individual spores mostly ellipsoid and (7–)8–10(–12) × 4–6 μm, frequently narrowed slightly near the middle, rounded distally, tapered slightly proximally to a broad, truncated attachment, occasionally broadly elliptic to subglobose and 8–10.5 × 7.5–10 μm; wall smooth, thick, appearing multilayered (Figs. 8, 9), inamyloid, acyanophilous.

Growing in pupal chambers and on the walls of larval galleries of *Dendroctonus ponderosae* Hopkins on *Pinus contorta* Dougl. var. *latifolia* Engelm. Sometimes growing beyond galleries and chambers if separation of bark and wood occurs.

SPECIMENS EXAMINED: On *Pinus contorta* var. *latifolia*; Indian Meadows near Riske Creek, B.C., Canada. VI.1977, Safranyik, Muraro, and Whitney (DAVFP 23158); 27.X.1977, Whitney (DAVFP 23159); partially insectary reared brood bolts collected X.1977 from Riske Creek, 12.V.1978, Elliot (DAVFP 23160); 12.VIII.1978, Whitney (DAVFP 23157 TYPE); Lye Lake near Riske Creek, VII.1982, Whitney, Safranyik and Moeck (DAVFP 23165); wood-block culture 7.VII.1982, Strongman (DAVFP 23167); Tyee Lake, B.C., 26.VI.1979, Whitney (DAVFP 23163); Gun Lake, B.C., 20.V.1978, Whitney (DAVFP 23161); Yaak River, 32 km N of Sylvanite, Montana, U.S.A., 12.VIII.1980, Whitney, Miller and Berryman (DAVFP 23164); on *Pinus ponderosa* Laws.; 1 km N of Clinton, B.C., 24.VI.1978, Whitney (DAVFP 23162).

In culture, the fungus fruits readily on autoclaved, freshly collected, inner bark and sapwood segments of *Pinus contorta* branches. Development appears to be identical with that in beetle galleries but more extensive. A thin, whitish mycelium, with narrow strands develops, reaching 2 cm in diameter in 5 days at 20°C. At this time, scattered clusters of cystidia and basidia are present near the inoculation point. Basidial production continues and the patches, interconnected by delicate strands, become hemispherical, then anastomose to produce a continuous hymenium. A gently undulating surface, reflecting basidiocarp development through anastomoses of the hemispherical initial fertile patches, is characteristic of cultures but was not seen in natural material.

In culture, as in material developed naturally, the hymenium thickens and the basidiocarp often shows some layering. A zone of loosely interwoven, primarily erect hyphae sometimes is present between the thin basal layer and the hymenium. In well-developed fructifications, the upper one-half to two-thirds of the total thickness consists of a thick but fragile crust of basidiospores. Monospore isolates yielded clampless mycelia, some of which had occasional false clamps.

Results and discussion

Clamp connections, dolipore septa (Fig. 5), and layered walls (Fig. 5) placed this fungus firmly in the Basidiomycotina. Spores borne on sterigmata of clavate sporogenous cells

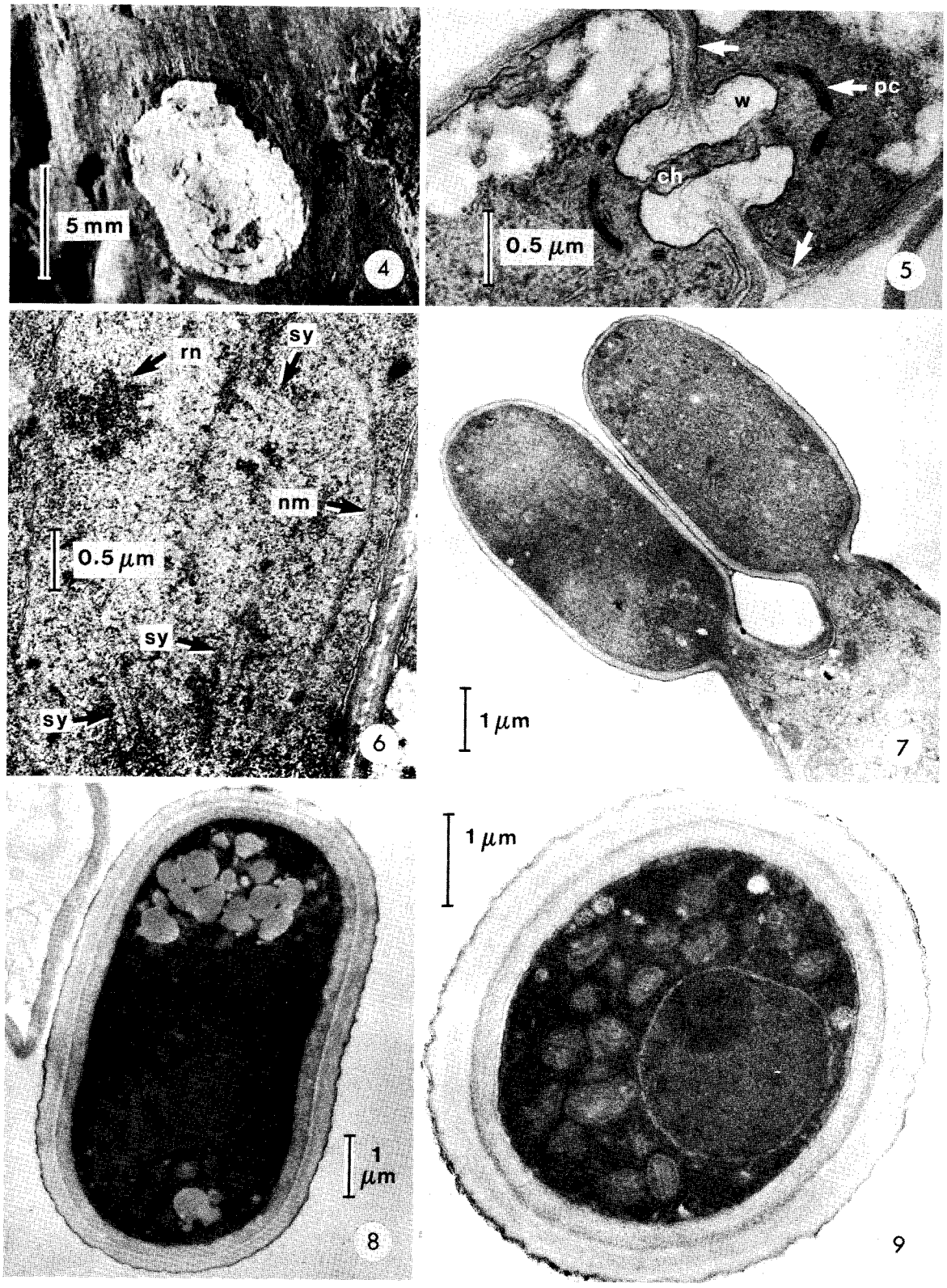

FIG. 4. Loose powdery mass of basidiospores of *Entomocorticium dendroctoni* in a mountain pine beetle pupal chamber. FIGS. 5–9. TEM photographs of *Entomocorticium dendroctoni*. Fig. 5. Median section of dolipore septum showing central channel (*ch*), septal wall swellings (*w*), and irregularly perforated parenthesome cap (*pc*). Note also multilayered cell walls (arrows). Fig. 6. Meiotic nucleus in a basidium, synaptinemal complexes (*sy*), remnant of nucleolus (*rn*), and nuclear membrane (*nm*). Fig. 7. Basidial apex with two young basidiospores symmetrically attached to two short stout sterigmata. Nuclei have not yet migrated into the spores. Fig. 8. Longitudinal section of a mature basidiospore. Note very thick wall and two nuclei present. Fig. 9. Transverse section of a mature basidiospore.

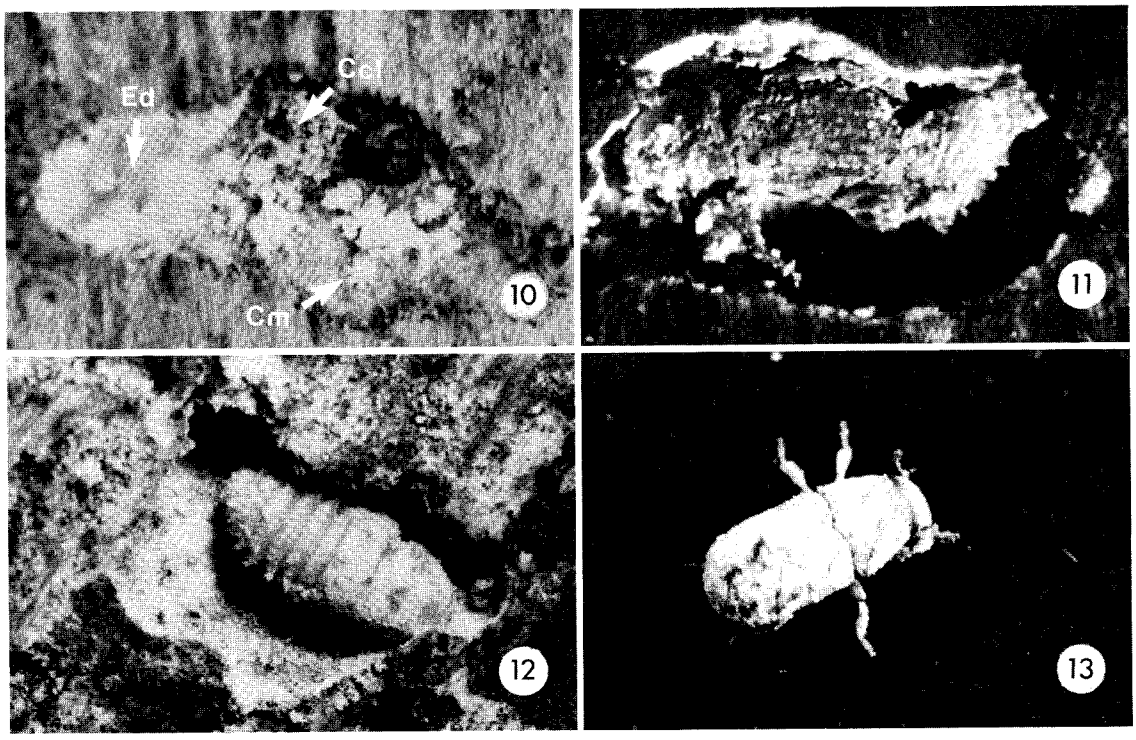

FIG. 10. Pupal chamber of mountain pine beetle containing *Entomocorticium dendroctoni* (Ed) and conidial masses of the blue stain fungi *Ceratocystis montia* (Cm) and *Ceratocystis clavigera* (Ccl.). ×6.5. FIG. 11. Cadaver of young mountain pine beetle adult colonized by *Entomocorticium dendroctoni*. ×6.5. FIGS. 12–13. Basidiospore-laden mountain pine beetles. Fig. 12. Pupa. ×6.5. Fig. 13. Young adult, preemergence. Emergent adults are normally shiny black. ×6.0.

gave further evidence of its basidiomycetous nature. However, absence of spore abstriction and spores borne symmetrically on broad sterigmata (Fig. 7) raised the possibility that the spores could be conidia and not basidiospores. Typical synaptinemal complexes were readily found in ultrathin sections of sporogenous cells in young sporocarps (Fig. 6). This showed that meiotic prophase nuclei were present and confirmed that these sporogenous cells were basidia. Lack of abstriction was likely inconsequential for spore dissemination because of the close spatial and temporal association of fungal sporulation to the dispersal stage of the mountain pine beetle.

The general features of *E. dendroctoni* basidiomata indicate a close link with taxa in the Croticiaceae, in which family the taxon should currently be placed. In our opinion, however, the absence of basidiospore abstriction, essentially sessile basidiospores, and the ecological and biological features linked to its association with beetles would seem to exclude the species from other genera currently recognized in the family. A similar fungus *Gloeocystidium ipidophilum*, was described from Poland by Siemaszko (1939). According to Siemaszko, the hymenium of this species contained both gloeocystidia and cystidia (neither of which were described as being incrusted), 1- to 2-spored basidia, and predominantly ellipsoid basidiospores. Spore abstriction was not mentioned, but the illustrations suggest absence of the feature. Thus, *E. dendroctoni* and *G. ipidophilum* would appear to be closely related and probably congeneric. They differ in the absence of gloeocystidia in *E. dendroctoni*, the absence of incrustation on cystidia of *G. ipidophilum*, the numbers of spores per basidium, and basidiospore form.

Entomocorticium dendroctoni was compared in YM culture with SJB 122 from the mycangium of *D. frontalis* and the unidentified basidiomycete from the mycangium and habitat of *D. brevicomis*. It was very different from these fungi. The cultures from the southern pine beetle and the western pine beetle were cerebroid, dark brown, and slow growing compared with the smooth surface, light tan, faster growing *E. dendroctoni*. No anastomosis was found on Y/M cocultures of *E. dendroctoni* and either SJB 122 or the unidentified basidiomycete from the western pine beetle. Whether *E. dendroctoni* is congeneric with one or both mycangial fungi awaits further study.

Pure cultures of *E. dendroctoni* were readily obtained from basidiospores or small pieces of basidiocarp on YM/10. However, attempts to isolate it from newly established adult beetles, from sapwood, or from phloem adjacent to galleries and pupal chambers, on several media, including a special basidiomycete medium (Castello *et al.* 1976), were unsuccessful.

A multispore isolate of *E. dendroctoni* was grown on several different media at 20°C and over a range of temperatures (10–27°C) on malt agar. Growth rates in millimetres per day were malt extract, 0.4; nutrient agar, 2.2; Czapek, 2.3; YM, 5.6; corn meal, 6.0; Sabouraud dextrose, 6.3; malt, 7.2; and potato dextrose, 8.1. On malt agar the fungus grew 1.9 mm/day at 10°C; 4.2 at 15°C; 7.1 at 20°C; 6.6 at 24°C; and 6.2 at 27°C. Growth measurements were terminated when the faster replicates had covered the agar surface. No sporulation occurred in any culture plates kept up to 6 weeks. However, as mentioned in the taxonomy section, basidiospores were readily produced when the fungus was cultured on autoclaved fresh pine wood.

Standard decay tests were not done, but observations suggested this basidiomycete was not an aggressive sapwood decayer. After 4 weeks at room temperature *E. dendroctoni* had not penetrated beyond 2 mm into the sapwood of autoclaved lodgepole pine wood blocks and furthermore this sap-

wood was firm when pried with the point of a knife.

Young adult mountain pine beetles eat the fungus lining of their pupal chambers (Whitney 1971). In the present study some pupal chambers were lined with *E. dendroctoni* (Figs. 3, 4), some with a mixture of the blue stain fungi *Ceratocystis clavigera* (Robinson-Jeffery and Davidson) Upadhyay and *C. montia* Rumb., and some with all three fungi sporulating abundantly (Fig. 10). The possible effect of these fungi on maturation and subsequent performance of mountain pine beetles was investigated by placing newly eclosed partially insectary reared adult beetles in three-dram vials with excised pupal chambers bearing copious spores. In a bioassay on fresh bolts, pairs of adult mountain pine beetles that had fed 15 days in the vials with *E. dendroctoni* produced, on average, 19% more eggs and larvae per gallery than did beetles fed blue stain fungi (Table 1). Both fungus-fed treatments produced significantly fewer eggs than did beetles fed fresh phloem. This may reflect ingestion of pathogens or parasites such as microsporidians or nematodes which are commonly present in natural bark beetle brood habitats and which are believed to reduce fecundity (Weiser 1970; Massey 1974). At the time of measurement the percent egg hatch was 59.1 on *E. dendroctoni*, 55.6 on blue stain fungi, and 67.5 on pine phloem. The overall effect on bark beetle bionomics of individual microorganisms in the diet of developing brood is likely very complex.

Cadavers of third- and fourth-instar larvae and of young untanned adults were occasionally found in the field colonized by *E. dendroctoni* (Fig. 11). In a preliminary test for pathogenicity of this basidiomycete, 20 newly eclosed unfed axenic adults were placed on wood block cultures of *E. dendroctoni* that had produced large amounts of basidiospores (Strongman 1982). The new adults became thoroughly inoculated externally and consumed most of the basidiospores in the cultures. There were no symptoms of disease in observations made up to 14 days. These beetles were then used in another experiment where they reproduced normally. This lack of disease is corroborated in the foregoing results where the beetles were fed gnotobiotic *E. dendroctoni* and also by the previous report by Strongman (1982) of successfully rearing axenic mountain pine beetle larvae to adults in the presence of a pure culture of *E. dendroctoni*.

It is most likely that *E. dendroctoni* is carried from tree to tree by attacking adult mountain pine beetles (Figs. 2, 12, 13). It may also be carried by mountain pine beetle insect associates and possibly by wind. Careful insect caging and fungus isolation work are needed to ascertain the mode of inoculation. Its role in the ecology of mountain pine beetles attacking lodgepole pine awaits further study.

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