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Clarification of the host substrate of *Ascopolyporus* and description of *Ascopolyporus philodendrus* sp. nov.

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Abstract: During a recent collection trip to Barro Colorado Island, Panama, two species belonging to genus *Ascopolyporus* (Clavicipitaceae, Hypocreales) were collected. Species of *Ascopolyporus* are epibionts of their bamboo (Poaceae) host and long thought to be biotrophs of their plant hosts. However, based on morphological observations and phylogenetic evidence using large subunit ribosomal DNA data, we propose that genus *Ascopolyporus* is likely composed of pathogens of scale insects (Coccoideae, Homoptera). Phylogenetic analyses included *Ascopolyporus* spp. in a clade containing only entomopathogenic clavicipitaceous species (100% posterior probability), and the scale insect pathogen *Hyperdermium bertonii* was found to share the most recent common ancestor with the *Ascopolyporus* clade (98% posterior probability). In addition remnants of the scale insect were observed to be embedded within stromata during early stages of stroma development. *Ascopolyporus philodendrus* sp. nov. was described and distinguished from the type species of the genus, *A. polychrous,* based on perithecial size, ascus size, plant host substrate and phylogenetic evidence. Furthermore subfamily Clavicipitoideae (Clavicipitaceae) was included and well supported in a single clade (100% posterior probability).

Key words: *Cordyceps,* endophyte, entomopathogen, epibiont, *Hyperdermium, Lecanicillium,* scale insect, *Torrubiella*

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INTRODUCTION

The fungal family Clavicipitaceae (Hypocreales, Ascomycota) is composed largely of pathogens and symbionts of plants, arthropods and fungi (Rogerson 1970). Much is known about the genera *Claviceps* Tul., *Balansia* Speg. and *Epichloë* (Fr.) Tul. due to their association with economically important grasses in subfamily Pooideae (Funk and White 1997, Schardl et al 1997). In addition a great deal is known about the diversity of arthropod and fungal pathogenic members of genera *Cordyceps* (Fr.) Link, *Torrubiella* Boud. and *Hypocrella* Sacc. due to the depth and breadth of many historical taxonomic studies (e.g. Petch 1921, Mains 1957, Kobayasi 1982, Kobayasi and Shimizu 1963). In contrast few investigations have been made into the ecology and systematics of the clavicipitaceous genera associated with bamboos and other economically unimportant hosts. The bamboo host niche encompasses nearly a third of all clavicipitaceous genera. Of these genera *Stereocrea* Sydow & Sydow, *Cavimalum* Doi et al, *Mycomalus* Möller, *Ascopolyporus* Möller and *Konradia* Raciborski are epibionts that develop on the culms of their hosts. Although originally considered pathogens of their plant substrates, many members of Clavicipitaceae have been found to be pathogens of homopterans (e.g. Coccoideae) that spend the majority of their life cycle attached to their plant host (Petch 1921, Hywel-Jones and Samuels 1998, Sullivan et al 2000, White et al 2002). Clavicipitaceous genera *Hyperdermium, Dussiella* (= *Echinodothis*) and *Fleisheria* Penzig & Sacc. (= *Hypocrella*) all were thought to be plant pathogens until they were discovered to be pathogens of scale insects or leaf-hoppers (Bischoff and White 2003).

During recent trips to Barro Colorado Island, Panama, two distinct species that were determined to belong to genus *Ascopolyporus* were collected. One strain was similar to the type species of the genus (*A. polychrous* Möller). The other strain had not developed perithecia but best could be identified as *A. villosus* Möller. The sequences of recently collected specimens of *A. polychrous* were provided to us by Kathie Hodge's lab at Cornell University.

Based on the distinction of the *Ascopolyporus polychrous*-like specimen from other *Ascopolyporus* species we describe a new species, *Ascopolyporus philodendrus*

J.F. Bisch. sp. nov. In addition we used large subunit (LSU) ribosomal DNA (rDNA) and morphological data to investigate affinity of *Ascopolyporus* to other clavicipitaceous genera.

MATERIALS AND METHODS

Vouchers.—Collections of *Ascopolyporus philodendrus* and *A. villosus* were made on Barro Colorado Island (BCI), Panama, in the summers of 2002 and 2003. In each case the material was brought to the field station and isolated on potato-dextrose agar (PDA, Difco Inc.) with antibiotics (gentamicin 40 mg/L, streptomycin 40 mg/L, penicillin 20 mg/L). Stromata were placed in vials of FAA (five parts stock formalin, five parts glacial acetic acid, 90 parts 50% ethyl alcohol) or 100% ethanol. Voucher material was deposited in the herbarium at the New York Botanical Gardens (NY).

Upon return to Rutgers University subcultures were made to potato-carrot agar (PCA) to enhance conidial development. Cultures were maintained at ca. 23 C under fluorescent lights. Conidial development occurred 7–12 d after subculturing. Cultures were submitted to the Agricultural Research Service's Collection of Entomopathogenic Fungal Cultures (ARSEF: *A. philodendrus* = 7354 and *A. villosus* = 6355).

Morphological observations.—Microscopic observations were made from squash mounts and sections. Sections of *Ascopolyporus philodendrus* were fixed and prepared as described by Sullivan et al (2000). Squash mounts were made from material stored in FAA and ethanol and from the culture isolations. Microscopic evaluations were made with a Zeiss Axioskop microscope. Macroscopic evaluations were made with a Zeiss Stemi SV8 dissecting scope. Photographs were taken with a Nikon® Coolpix 880 digital camera.

Sequence data.—Fresh mycelium was taken from cellulose acetate sheets overlaid on PDA and ground with liquid nitrogen. Genomic DNA was extracted with the DNeasy® Plant Mini Kit (QIAGEN). The rDNA ITS2 and the 5′ end of 28S regions were amplified from 4 μL of genomic DNA using primers ITS5 (Vilgalys and Hester 1990) and LR7SM (Sullivan et al 2000) in a 50 μL reaction. PCR reactions and cycle sequencing reactions were performed as described by Sullivan et al (2000) and analyzed on an ABI 3100 Automated DNA Sequencer. LSU sequences of *Ascopolyporus philodendrus* (AY886545), *A. polychrous* (AY886547) and *A. villosus* (AY886544) were submitted to GenBank. Sequences obtained from GenBank for phylogenetic analysis are provided (TABLE I).

Phylogenetic analysis.—Sequencher (Genecodes, Ann Arbor, Michigan) was used to analyze, edit and construct consensus sequences from sequence products. Matrix alignment was performed in Clustal X (Thompson et al 1997) using the default settings. The alignment was checked and improved manually. The alignment is available at Tree Base.

Modeltest 3.06 (Posada and Crandall 1998) was used to select the model of evolution that best fit the data. This model was input into PAUP 4.0b10 Alvitec (Swofford 2002). A maximum likelihood analysis was performed with model parameters invariable sites (I), gamma distribution (G), base frequencies and the R matrix as determined by Modeltest. Taxa were added randomly in 100 replicates with a random starting seed. One tree was held at each step during stepwise addition using the TBR algorithm. Branches were collapsed if branch length was less than or equal to 1^{-10}.

MrBayes 3.0, a Bayesian phylogenetic inference program (Huelsenbeck and Ronquist 2001), was used to determine branch support (posterior probabilities). Bayesian analysis was run with four Markov chains Monte Carlo (three cold, one heated) for 2 000 000 generations, sampling every 100 generations (including the first generation), which yielded 20 001 trees. These trees were graphed to determine at which point the trees being recovered were asymptotic (approaching a constant state). The trees that were not asymptotic were discarded (''burn-in'', Huelsenbeck 2000). Bayesian analysis was done five times to get a broad spectrum of likely trees. These trees were imported into PAUP 4.0b10 Alvitec (Swofford 2002) and a majority-rule consensus tree was produced to determine posterior probabilities. Support values are reported on the maximum likelihood tree (FIG. 3).

TAXONOMY

Ascopolyporus philodendrus J.F. Bischoff sp. nov. FIG. 1A–H

Stromate tuberose-globoso vel ungulatum, 12–25 mm longis et 12–20 mm crassis, roseo dein flavido, puncto centrali affixo; supra sterile, infra fertile. Peritheciis confertis, immerses, 200–300 μm longis et 40–80 μm crassis. Ascis cylindraceis, 90–140 μm longis et 3–5 μm crassis; ascosporae, filiformes, hyalina, longitudine ascorum. Conidiophora phialidica, hyaline, discreta, singularis, determinate, 30–60 μm × 1–3 μm; conidia enteroblastica, subcylindrica, hyaline, asepta vel multisepta, 7–25 × 2–5 μm, capitata.

Stromata epibiotic on stem, subglobose (immature) to polypore-like (mature), 12–25 mm wide and 12–20 mm high; upper surface sterile, red-purple; lower surface ascomatous, fertile, white to tan. Perithecia immersed, crowded, obclavate, 200–300 × 40–80 μm; ascus cylindrical, 90–140 × 3–5 μm, with thickened perforated apical tip; ascospores filiform, length of ascus. Conidiogenous cells (from culture) simple, phialidic, hyaline, 30–60 × 1–3 μm, with collarets at tip. Conidia (from culture) enteroblastic, subcylindrical, 0–4 septa, accumulating in head at phialidic tip, 7–25 × 2–5 μm. Conidiogenous cells and conidia arise from surface of stroma.

Habit. Stem of lianoid *Philodendron* sp. (Araceae).

Holotype. Panama, Canal Zone: Barro Colorado Island, Jul 2002, J.F. Bischoff (JB122), stored at the New York Botanical Gardens (NY).

Remarks.—*Ascopolyporus philodendrus* most closely resembles Möller's (1901) description of *A. polychrous* in stroma

TABLE I. Large Subunit Ribosomal DNA sequences included in analyses

Taxa	Genbank accession	Taxa	Genbank accession
Ascopolyporus philodendrus J.F. Bisch. & J. White	AY886545	*Cordyceps pruinosa* Petch	AB044635
Ascopolyporus polychrous Moller*	AY886547	*Cordyceps ramosopulvinata* Y. Kobayasi & D. Shi	AB027372
Ascopolyporus villosus Moller*	AY886544	*Cordyceps subsessilis* Petch	AF373285
Atkinsonella hypoxylon (Pk.) Diehl	U57087	*Dussiella tuberiformis* (Berk. & Rav) Atk.	U57083
Atricordyceps harposporifera Samuels	U17400	*Epichloë amarillans* J.F. White	U57680
Balansia henningsiana (Möller) Diehl	U57678	*Epichloë typina* (Pers.:Fr.) Tul.	U17396
Balansia obtecta Diehl	U17395	*Hyperdermium bertonii* (Speg.) J.F. White et al.	AF242354
Balansia strangulans (Mont.) Diehl	U57679	*Hyperdermium pulvinatum* J.F. White et al.	AF242353
Beauveria bassiana (Bals.) Vuill.	AF245300	*Lecanicillium antillanum* Castaŋeda & G. Arnold	AF339536
Beauveria brongniartii (Sacc.) Petch	AB027381	*Lecanicillium aranearum* (Petch) W. Gams	AF339537
Chaunopycnis alba W. Gams	AF245296	*Lecanicillium fusisporum* W. Gams	AF339549
Chaunopycnis sp.	AF245297	*Lecanicillium lecanii* (Zimm.) Viegas	AF339555
Claviceps fusiformis Loveless	U17402	*Leuconectria clusiae* (Samuels & Rogerson) Rossman et al.	U17412
Claviceps paspali F. Stevens & J.G. Hall	U47826	*Nectia radicicola* Gerlach & L. Nilsson	U17415
Claviceps purpurea (Fr.) Tul.	U57085	*Nectria cosmariospora* De Not & Ces. Schema	U17407
Cordycepioideus bisporus Stifler	AF009654	*Neomunkia sydowii* Petrak	AY327047
Cordyceps capitata (Fr.) Link	U57086	*Neotyphodium coenophialum* A.E. Glenn et al.	U57681
Cordyceps inegoensis Kobayasi	AB027368	*Polycephalomyces ramosus* (Peck) Mains	AY259543
Cordyceps japonica Lloyd	AB027367	*Tolypocladium cylindrosporum* W. Gams	AF245301
Cordyceps jezoensis Kobayasi	AB027365	*Torrubiella luteorostrata* Zimm.	AF327388
Cordyceps kanzasiana Kobayasi & Shimizu	AB027371	*Torrubiella piperis* J.F. Bisch. & J. White	AY466442
Cordyceps militaris (L.) Link	AF043135	*Ustilaginoidea dichromenae* P. Henn.	AF373280
Cordyceps ophioglossoides (Ehrenberg) Link	U47827	*Ustilaginoidea virens* (Cooke) Takah.	AF245299
Cordyceps prolifica Kobayasi	AB027370		

* Indicates strains sequenced for this study.

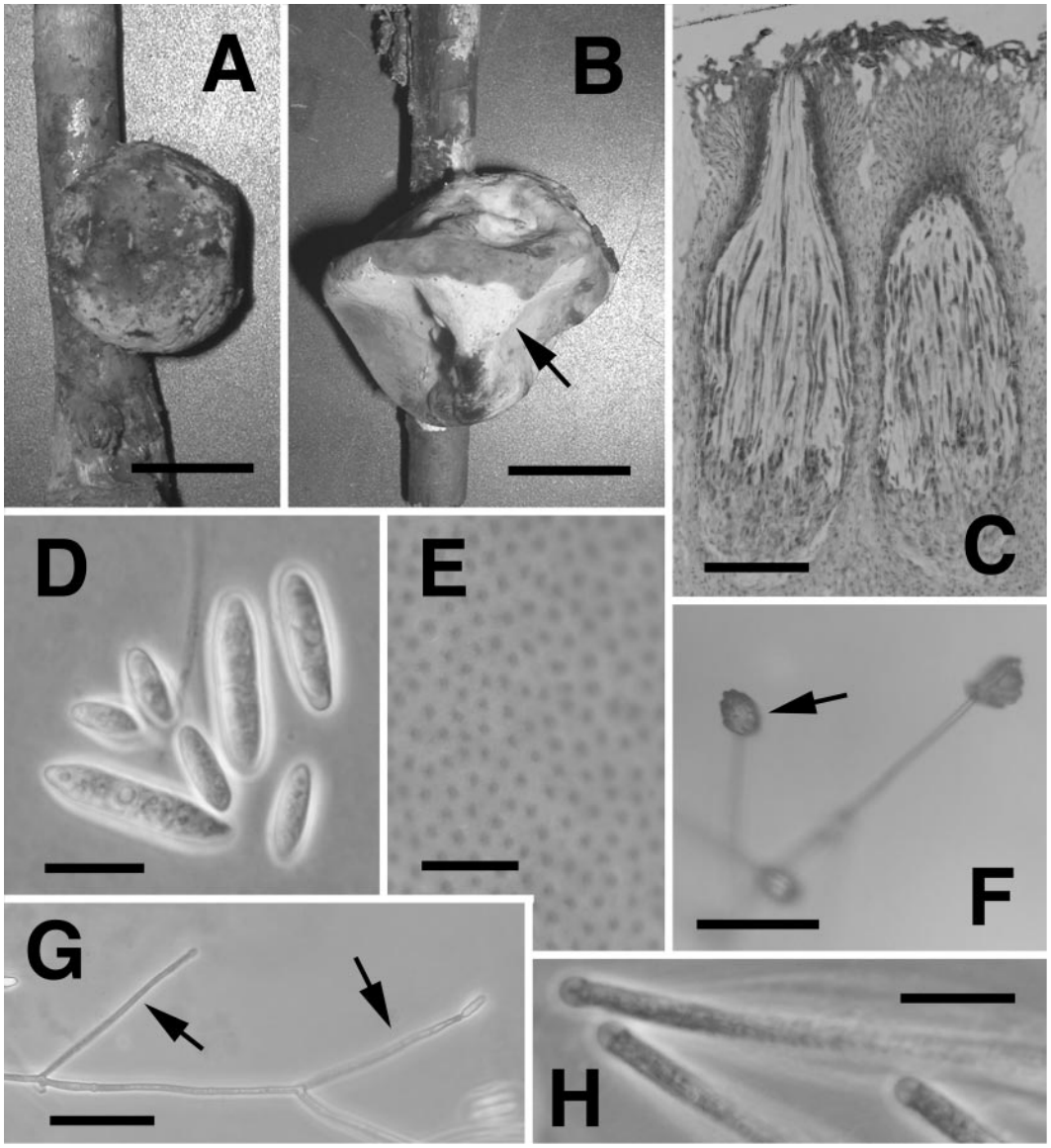

FIG. 1. *Ascopolyporus philodendrus*. A. Immature stroma on *Philodendron* sp. stem. Bar = 10 mm. B. Mature stroma with fertile ascomata (arrow). Bar = 10 mm. C. Perithecia. Bar = 150 μm. D. Conidia (phase contrast). Bar = 10 μm. E. Immersed perithecia of lower surface of stroma. Bar = 50 μm. F. Phialide apex with conidial head (arrow). Bar = 50 μm. G. Simple conidiophore (arrow). Bar = 25 μm. H. Top portion of asci. Bar = 20 μm.

color, polypore-like form and conidial morphology. However Möller described the size of the perithecia (~750 μm long), asci (~500 × 4 μm), and ascospores (~300 × 1 μm) of *A. polychrous* to be larger than found in *A. philodendrus*. Furthermore, unlike other *Ascopolyporus* species, *A. philodendrus* was collected from *Philodendron* sp. (Araceae). All other *Ascopolyporus* taxa were found attached to bamboos (Poaceae).

RESULTS

Morphology.—Both *Ascopolyporus* spp. developed epibiotically from the stem of the host plant. *Ascopolyporus philodendrus* (FIG. 1A–H) was found on a liana (*Philodendron* sp.) approximately 0.5–2 m above ground. *Ascopolyporus villosus* (FIG. 2A–F) was found growing 3–20 cm above ground on the culm of an unidentified *Chusquea* species. *Ascopolyporus philodendrus* was red to purple, and *A. villosus* was white to pale yellow. Perithecia developed on the underside of the *A. philodendrus* stroma so that the ostioles were facing the ground. No perithecia were observed on any *A. villosus* stromata.

The conidiogenous cells of both *Ascopolyporus philodendrus* and *A. villosus* are phialidic. The phialides

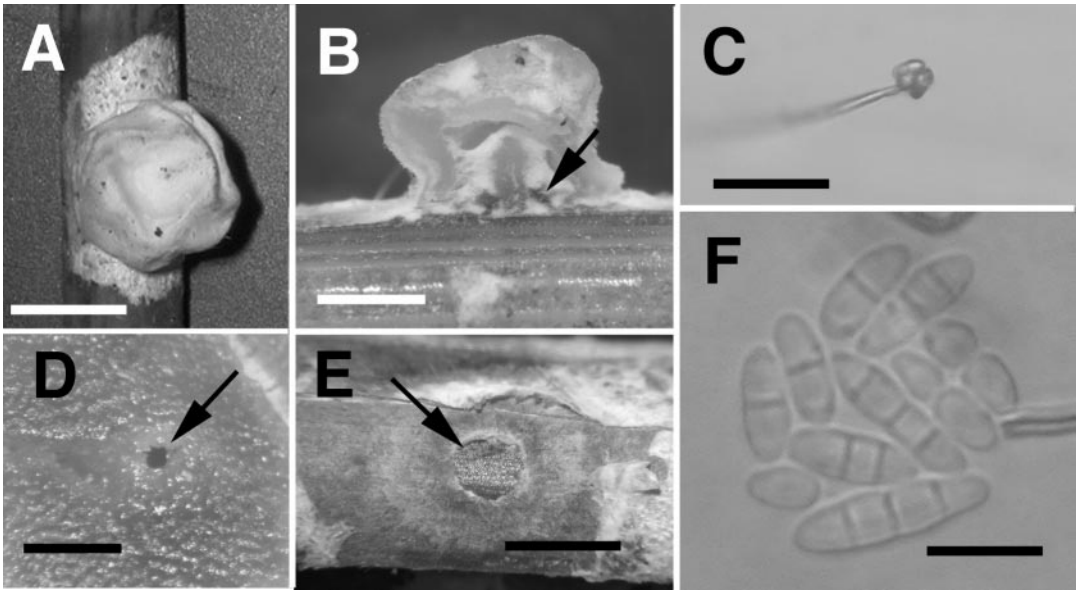

FIG. 2. *Ascopolyporus villosus*. A. Stroma on *Chusquea* sp. culm. Bar = 6 mm. B. Transverse section of the stroma showing remnants of scale insect lenticular derm (arrow). Bar = 2 mm. C. Phialide apex with conidial head. Bar = 40 μm. D. Underside of fungal stroma with round hole (arrow) from which scale insect stylet protruded and entered plant substrate. Bar = 200 μm. E. Subiculum on culm after stroma has been removed and exposing scale insect "footprint" (arrow). Bar = 2 mm. F. Conidia (bright field). Bar = 12 μm.

arise from the young stroma (FIGS. 1F, G; 2C). Both species produce enteroblastic, subcylindrical, guttulate conidia (FIGS. 1D, 2F). Immature conidia are single celled. However they elongate and develop 1–4 septa during maturation (FIG. 2C). Mature conidia of *A. philodendrus* measure 12–25 × 3–4 μm (FIG. 1D). Mature conidia of *A. villosus* measure 10–22 × 2–5 μm (FIG. 2F).

The lenticular shape of what remained of the scale insect host test was observed in several young *Ascopolyporus villosus* stromata (FIG. 2B). When stromata were removed from their respective plant substrates a circular gap in the mycelium was observed directly below the position where the scale insect once was attached (FIG. 2E). On the underside of several stromata in the ellipsoidal region where the scale insect was attached we saw a small round hole (ca. 40–50 μm diam) where the thread-like mouthparts likely were inserted into the plant (FIG. 2D).

Phylogenetic analysis.—The matrix contained sequences of 47 taxa, 44 of which were obtained from GenBank (TABLE I). A total of 885 characters were aligned homologously. Modeltest 3.06 concluded that the General Time Reversible model with invariable sites and gamma distribution values included (GTR + I + G, Tamura and Nei 1993) was the model of evolution that best fit the data based on the Akaike Information Criterion (AIC Akaike 1974). The parameters included: base frequencies A = 0.2432, C = 0.2357, G = 0.3242, T = 0.1969; rate matrix A↔C = 0.6805, A↔G = 2.6668, A↔T = 0.5044, C↔G = 1.1617, C↔T = 9.9513, G↔T = 1.0000; I = 0.6376, G = 0.6363.

Of the 100 005 trees sampled from 10 000 005 generations 4048 were discarded due to "burn-in", leaving 95 957 trees to generate posterior probability values (FIG. 3). PAUP found the most likely tree (−ln 4331.55920 FIG. 3) in three of 100 replicates.

Members of Clavicipitaceae (Clades A, B, C) were supported as a monophyletic grouping (100% posterior probability). Clade A was weakly supported (<50% posterior probability). The relationships among many groups within Clade A and how they relate to Clade B varied greatly among the trees reported by Bayesian analysis (not shown). Clade B itself was well supported (100% posterior probability) as a distinct group within Clavicipitaceae. Clade B contained entomogenous taxa in genera *Cordyceps, Hyperdermium, Lecanicillium* W. Gams & Zare, *Beauveria* Vuill. and *Ascopolyporus*. Species of *Ascopolyporus* were supported as a monophyletic grouping (100% posterior probability) with *Hyperdermium bertonii* in the ancestral position of the clade (98% posterior probability). Phylogenetic analyses suggest that clades A and B are more closely related to each other than either is to members of Clade C (72% posterior probability). Clade C was supported as a monophyletic group with 100% posterior probability. This

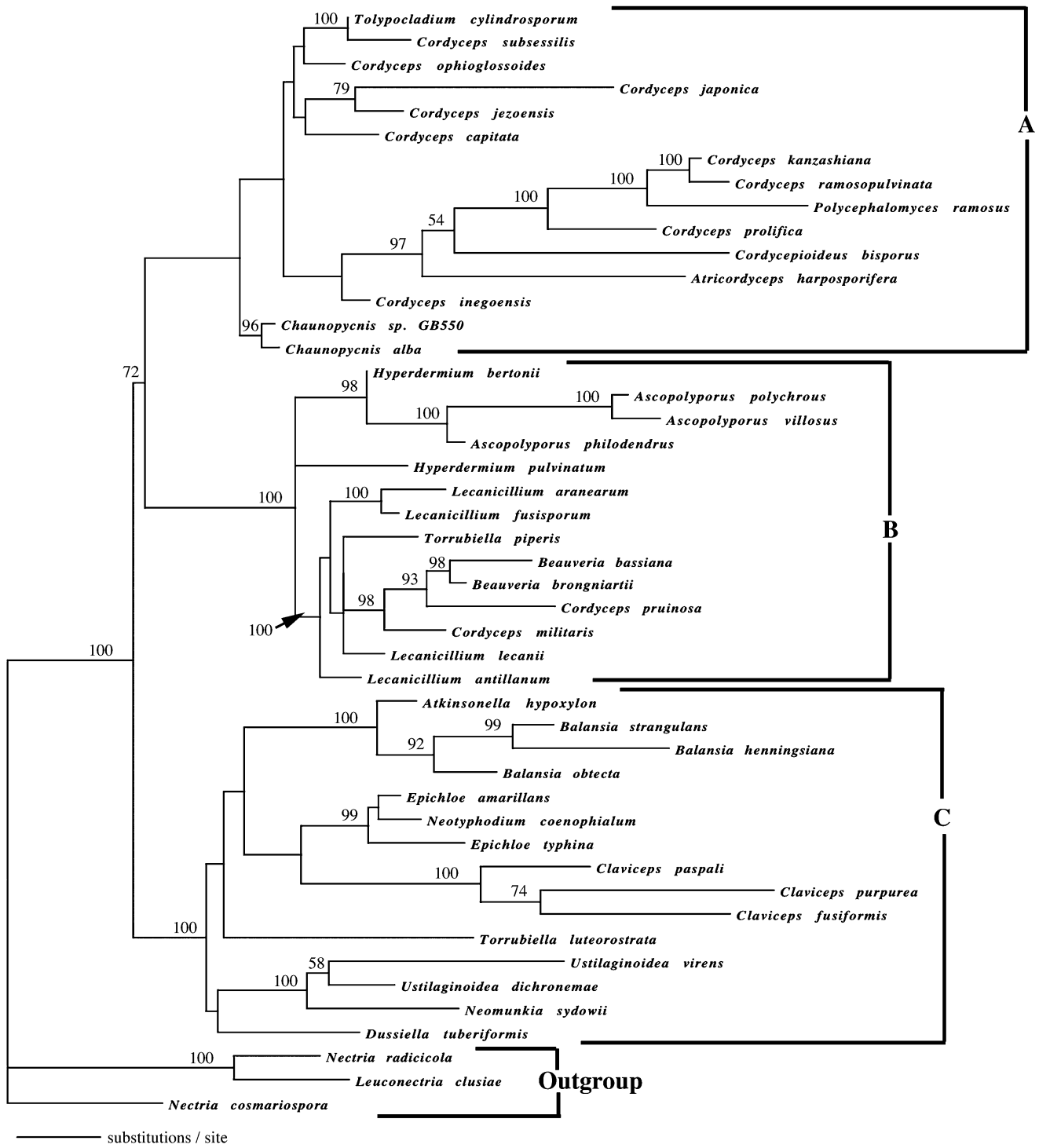

FIG. 3. The most likely tree (−ln 4331.5592) as determined by PAUP Alvitec 4.0b10 using GTR + I + G model of evolution. The numbers on the branches indicate the posterior probability as a percentage for the node they proceed (only ≥50% shown).

clade contains all of the clavicipitaceous plant pathogens and symbionts included in this analysis. The only entomopathogens in Clade C are *Dussiella tuberiformis* and *Torrubiella luteorostrata*.

DISCUSSION

Nutrition acquisition.—Species of *Ascopolyporus* were thought to be pathogens of their plant host (Roger-

son 1970). However Bischoff and White (2003) hypothesized that the genus might be necrotrophs of scale insects (Coccoidea). The remains of what best could be determined to be the test of the scale insect (FIG. 2B) and the stylet hole (FIG. 2D) in the base of the stroma provide physical evidence of insect parasitism. The inclusion of genus *Ascopolyporus* among entomopathogenic members of Clavicipitaceae (FIG. 3, Clade B, 100% posterior probability) also supports the scale insect parasitism hypothesis of *Ascopolyporus*. Clades A and B contain only insect pathogens and mycoparasitic members of Clavicipitaceae while all the known plant pathogens and symbionts of the family are found in Clade C (100% posterior probability). The hypothesis is further strengthened by the close relationship of *Ascopolyporus* to the scale insect pathogenic genus, *Hyperdermium,* especially its type species, *H. bertonii* (98% posterior probability). Conidial morphology and epibiotic habit of both genera support the close relationship of *Ascopolyporus* and *Hyperdermium* (FIGS. 1A, B, D; 2A, E) (Sullivan et al 2000). These taxa are the only genera in Clavicipitaceae to produce multiseptate conidia (Möller 1901, Sullivan et al 2000). The conidia of *Hyperdermium* spp. are also subcylindrical, elongate with age and produced from simple conidiophores found on the stroma surface.

The relatively large size of *Ascopolyporus* spp. (reaching <4 cm diam, Bischoff and White 2003) in relation to its scale insect host (ca. 2–3 mm) also is interesting. Sullivan et al (2000) in discussing the nutritional associations of *Hyperdermium* spp. with their plant host suggested that the fungus first might consume the scale insect and then continue to garner nutrients from the plant through the hole left by the insect. This might account for the large stroma size of *Ascopolyporus* spp. in comparison to their insect hosts.

Immature stromata of Ascopolyporus philodendros are filled with a loose mycelial network and with large quantities of purple liquid, presumably composed of plant sap and fungal compounds. The plant sap likely emerges to the stroma through the stylet hole of the scale insect. The surface of the stroma is formed by the growth of mycelium on the surface of the liquid exudates from the plant. Young stromata of *A. philodendrus* are large and globose. The relatively large size of the stromata might be a function of the rich nutrient supply from plant sap and perhaps some physical force exerted from the volume of sap emerging from the plant. Development of perithecia occurs concurrently with deflation of the globose stroma, which assumes an angular shape, presumably, due to withdrawal of the liquid nutrient supply from the interior of the stroma. Why perithecia tend to form only the lower side of stromata is unknown.

Anamorphic states.—Members of *Ascopolyporus* and *Hyperdermium* are the only taxa in Clavicipitaceae, to our knowledge, to produce conidia that develop multisepta. Thus conidial morphology of *Ascopolyporus* and *Hyperdermium* appears to correspond with phylogenetic relationship. However the same is not true for the rest of the taxa in Clade B (FIG. 3). The orientation of taxa in the clade suggests a trend toward more derived phialide morphology. The simple *Cylindrocarpon*-like phialides of *Ascopolyporus* and *Hyperdermium* appear to be basal to the slightly more complex verticillate branching pattern (e.g. *Lecanicillium* spp.) and then *Beauveria* with its flask-shaped phialides and sympodial phialide tips. It will be interesting to see if monophyletic groups that share conidial morphology become apparent with the addition of more taxa that belong to this lineage.

Plant associates of Clavicipitaceae.—Diehl (1950) included the plant symbionts and biotrophs of Clavicipitaceae in subfamily Clavicipitoideae. All members of this subfamily grouped in Clade C (100% posterior probability, FIG. 3) in our analysis. This suggests that a single event led to plant symbiosis and biotrophism in Clavicipitaceae. However the Clavicipitoideae was not found to be monophyletic because it included the entomopathogens *Dussiella tuberiformis* and *Torrubiella luteorostrata* in deeply rooted positions. Both of these species are entomopathogens of scale insects. This suggests that scale insect pathogens could have been ancestor to the plant parasites and infection of scale insects might have been the evolutionary intermediate step from insect parasitism to plant parasitism in the family Clavicipitaceae. This hypothesis is further supported by the placement of the scale insect pathogens of Clade B, including *Ascopolyporus* spp., *Hyperdermium* spp., *Lecanicillium lecanii* and *Torrubiella piperis,* ancestors of *Beauveria bassiana* which Wagner and Lewis (2000) have shown to live endophytically in corn (*Zea mays*).

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LITERATURE CITED

Akaike H. 1974. A new look at the statistical model identification. IEEE Trans Auto Control 19:716–723.

Artjariyasripong S, Mitchell JI, Hywel-Jones NL, Gareth Jones EB. 2001. Relationship of the genus *Cordyceps* and related genera, based on parsimony and spectral analysis of partial 18S and 28S ribosomal gene sequences. Mycoscience 42:503–517.

Bacon CW, Porter JK, Robbins JD. 1975. Toxicity and occurrence of *Balansia* on grasses from toxic fescue pastures. Appl Microb 29:553–556.

Barker GM, Pottinger RP, Addison PJ. 1984. Effect of *Lolium* endophyte fungus infections on survival of larval Argentine stem weevil. NZ J Ag Res 27:279–281.

Bischoff JF, White JF Jr. 2003. The plant-infecting clavicipitaleans. In: White JF Jr, Bacon CW, Hywel-Jones NL, Spatafora JW, eds. Clavicipitalean fungi: evolutionary biology, chemistry, biocontrol, and cultural impacts. Marcel Dekker, USA.

Diehl WW. 1950. *Balansia* and the Balansiae in America. U.S. Department of Agriculture, USA.

Funk CR, White JF Jr. 1997. Use of natural and transformed endophytes for turf improvement. In: Bacon CW, Hill NS, eds. Neotyphodium/grass interactions. Plenum Press, USA. p 229–239.

Huelsenbeck JP. 2000. MrBayes: Bayesian inference of phylogeny. Distributed by the author. Department of Biology, University of Rochester, USA.

———, Ronquist F. 2001. MrBayes: Bayesian inference of phylogenetic trees. Bioinfomatics 17:754–755.

Kobayasi Y. 1982. Keys to the taxa of the genera *Cordyceps* and *Torrubiella*. Transactions of the Mycological Society of Japan 23:329–364.

———, Shimizu D. 1963. Monographic studies of *Cordyceps* 2. Group parasitic on Cicadidae. Bulletin of the National Science Museum of Tokyo Series B 6:286–314.

Mains EB. 1954. Species of *Cordyceps* parasitic on *Elaphomyces*. Bulletin of the Torrey Botanical Club 84:243–251.

Möller A. 1901. Phycomyceten und Ascomyceten, Untersuchungen aus Brasilien, Bot Mittheilungen aus den Tropen, Heft 9.

Petch T. 1921. Studies in entomogenous fungi: II. The genera *Hypocrella* and *Aschersonia*. Annals of the Royal Botanical Garden, Peradeniya 7:167–278.

Posada D, Crandall KA. 1998. Modeltest: testing the model of DNA substitution. Bioinformatics 14:817–818.

Rogerson CT. 1970. The hypocrealean fungi (Ascomycetes, Hypocreales). Mycologia 62:864–910.

Schardl CL, Phillips TD. 1997. Protective grass endophytes: Where are they from and where are they going? Plant Dis 81:430–438.

Sullivan RF, Bills GF, Hywel-Jones N, White JF Jr. 2000. *Hyperdermium*: a new clavicipitalean genus for some tropical epibionts of dicotyledonous plants. Mycologia 92: 908–918.

Swofford DL. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and other methods), Version 4.0b10 (Alvitec). Sinauer Associates, USA.

Tamura K, Nei M. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Mol Bio Evol 10:512–526.

Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG. 1997. The Clustal X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acid Res 24:4876–4882.

Vilgalys R, Hester M. 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. J Bacteriol 172:4238–4246.

Wagner BL, Lewis LC. 2000. Colonization of corn, *Zea mays*, by the entomopathogenic fungus *Beauveria bassiana*. App Enviro Microb 66:3468–3473.

White JF Jr. 1993. Structure and mating system of the graminicolous fungal epibiont *Echinodothis tuberiformis* (Clavicipitales). Am J Bot 80:1465–1471.