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Phylogeny and taxonomy of *Echinodontium* and related genera

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ABSTRACT
The phylogenetic relationship of eight species of *Echinodontium, Laurilia*, and *Perplexostereum* of Russulales were analyzed based on sequences of the nuc rDNA ITS1-5.8S-ITS2 (ITS [internal transcribed spacer]) and D1–D2 domains of nuc 28S rDNA (28S). Our results show that *Echinodontium tinctorium, E. ryvardenii*, and *E. tsugicola* represent *Echinodontium* sensu stricto. Based on morphological and phylogenetic evidence, the new genus *Echinodontiellum* is established to accommodate *Echinodontium japonicum. Amylostereum, Echinodontium, Echinodontiellum*, and *Larssoniporia* form the Echinodontiaceae clade. The Bondarzewiaceae clade includes *Bondarzewia, Heterobasidion, Laurilia*, and *Lauriliella*. The new genus *Lauriliella* is established for the species initially described as *Stereum taxodii* and *Lauriliella taiwanensis* new to science. The monotypic genus *Perplexostereum* forms a distinct clade. A key to the genera in the Echinodontiaceae and Bondarzewiaceae as well to *Perplexostereum* is provided.

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INTRODUCTION

Species of *Echinodontium* sensu lato are characterized by conspicuous basidiocarps, dentate to smooth hymenophores, encrusted cystidia, and ornamented, amyloid basidiospores. In Gross's (1964) monograph of the Echinodontiaceae, he included six species in *Echinodontium* Ellis & Everh. Later, Bernicchia and Piga (1998) added a new species, *E. ryvardenii* Bernicchia & Piga. Among these species, *E. sulcatum* (Burt) H.L. Gross and *E. taxodii* (Lentz & H.H. McKay) H.L. Gross were also placed in *Laurilia* Pouzar by some mycologists (Pouzar 1959; Parmasto 1968; Eriksson and Ryvarden 1976; Chamuris 1988; Ginns and Lefebvre 1993; Stalpers 1996).

Although similar in some characters, the type species of *Echinodontium* and *Laurilia* can be easily distinguished in morphology. *Echinodontium tinctorium* (Ellis & Everh.) Ellis & Everh. has pileate to ungulate basidiocarps, a coarsely dentate hymenophore, brick red–colored context, and a dimitic hyphal system. In contrast, *Laurilia sulcata* (Burt) Pouzar has resupinate to effuse-reflexed basidiocarps, smooth to tuberculate hymenophore, beige subiculum, and a trimitic hyphal system (Gross 1964; Eriksson and Ryvarden 1976; Stalpers 1996).

Ryvarden and Tutka (2014) proposed a new genus, *Perplexostereum* Ryvarden & S. Tutka, for *Stereum endocrocinum* Berk. Like *Echinodontium* and *Laurilia*, *Perplexostereum* develops large, pileate basidiocarps and ornamented amyloid basidiospores and inhabits gymnosperms but differs in lacking encrusted cystidia.

Tabata et al. (2000) demonstrated that *Echinodontium* and *Amylostereum* Boidin were phylogenetically related and belonged in the Echinodontiaceae. This was confirmed by subsequent studies (Hibbett et al. 2000; Hibbett and Donoghue 2001; Binder and Hibbett 2002; Hibbett and Binder 2002; Binder et al. 2005; Chen et al. 2016). However, *Echinodontium* was also shown to be closely related to *Bondarzewia* Singer and *Heterobasidion* Bref. in the Bondarzewiaceae/Echinodontiaceae clade by Larsson and Larsson (2003) and Miller et al. (2006). In addition, some of these studies showed that *Laurilia* and *Echinodontium* were closely related and possibly congeneric (Hibbett and Donoghue 2001; Hibbett and Binder 2002; Larsson and Larsson 2003; Binder et al. 2005; Miller et al. 2006).

We wanted to explore and clarify the phylogenetic relationship of *Echinodontium*, *Laurilia*, and *Perplexostereum* within Russulales by employing and analyzing sequence data of the nuc rDNA ITS1-5.8S-

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Supplemental data for this article can be accessed on the publisher's Web site.

ITS2 (ITS [internal transcribed spacer]) and D1–D2 domains of nuc 28S rDNA (28S). We include morphological, distributional, and ecological data to characterize the taxa in these genera. A key to the genera in the Echinodontiaceae and Bondarzewiaceae as well to the taxa discussed herein is provided.

MATERIALS AND METHODS

The specimens and cultures examined are deposited at the herbaria of Institute of Microbiology, Beijing Forestry University (BJFC); Center for Forest Mycology Research, U.S. Forest Service (CFMR); and National Museum of Natural Science, Taiwan (TNM). Samples for microscopic examination were mounted in cotton blue, Melzer's reagent, or 1% phloxine and studied at magnifications up to 1000× using a Nikon Eclipse 80i microscope (Nikon Corporation, Japan). Drawings were made with the aid of a drawing tube. The following abbreviations are used: L = mean spore length, W = mean spore width, Q = L/W ratio, n (a/b) = number of spores (a) from number of specimens (b), KOH = 2% potassium hydroxide. Color codes and names follow Kornerup and Wanscher (1978).

The ITS and 28S gene regions were amplified from cultures or a small piece of herbarium specimens using a cetyltrimethylammonium bromide (CTAB) rapid plant genomic DNA extraction kit (Aidlab, Beijing, China). The primers ITS5 and ITS4 (White et al. 1990) were employed to amplify the ITS region by using the following cycling protocol: initial denaturation at 95 C for 4 min, followed by 34 cycles at 94 C for 40 s, 58 C for 45 s, and 72 C for 1 min, and a final extension of 72 C for 10 min. The 28S gene region was amplified with primer pair LR0R and LR7 (http://www.biology.duke.edu/fungi/mycolab/primers.htm), using the following procedure: initial denaturation at 94 C for 1 min, followed by 34 cycles at 94 C for 30 s, 50 C for 1 min, and 72 C for 1.5 min, and a final extension of 72 C for 10 min. DNA sequencing was performed at Beijing Genomics Institute, China, using the same primers. Newly generated sequences were deposited in GenBank (SUPPLEMENTARY TABLE 1).

The phylogeny of Russulales was inferred from ITS and 28S sequence data. Sequences obtained from GenBank were primarily from Larsson and Larsson (2003; SUPPLEMENTARY TABLE 1). *Sistotrema brinkmannii* (Bres.) J. Erikss. and *S. muscicola* (Pers.) S. Lundell were selected as outgroup taxa following Larsson and Larsson (2003). The ITS and 28S sequences were aligned separately by using MAFFT 6 with a LINSI option (Katoh and Toh 2008; http://mafft.cbrc.jp/alignment/server/). The sequences were adjusted in BioEdit 7.0.5.3 (Hall 1999) and then concatenated manually. The concatenated alignments were deposited at TreeBase (http://treebase.org/treebase-web/home.html; submission ID 21276).

Maximum likelihood (ML), maximum parsimony (MP), and Bayesian inference (BI) analyses were performed for the data set by using RAxML 7.2.6 (Stamatakis 2006), PAUP* 4.0b10 (Swofford 2002), and MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003), respectively. In ML analysis, statistical support values (LB) were obtained by using rapid bootstrapping with 1000 replicates, with default settings used for other parameters. In MP analysis, gaps in the alignments were treated as missing data. Trees were generated using 100 replicates of random stepwise addition of sequence and tree bisection reconnection (TBR) branch-swapping algorithm, with all characters given equal weight. Branch supports (PB) for all parsimony analyses were estimated by performing 1000 bootstrap replicates (Felsenstein 1985) with a heuristic search of 10 random-addition replicates for each bootstrap replicate. The tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC), and homoplasy index (HI) were calculated for each generated tree. For Bayesian inference (BI), best models of evolution were obtained using MrModeltest 2.2 (Nylander 2004), and posterior probabilities (PP) were obtained by Markov chain Monte Carlo sampling in MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). Four simultaneous Markov chains were run for 5 million generations for the data set, and trees were sampled every 100th generation. The first quarter of the trees, which represented the burn-in phase of the analyses, were discarded, and the remaining trees were used to calculate posterior probabilities in the majority rule consensus tree.

RESULTS

Twelve ITS and 15 28S sequences were generated for this study. The data set contained 69 samples representing 53 ingroup and 2 outgroup taxa (SUPPLEMENTARY TABLE 1). The data set had an aligned length of 2442 characters, of which 840 were parsimony informative. MP analysis yielded 90 parsimonious trees (TL = 5372, CI = 0.390, RI = 0.572, RC = 0.223, HI = 0.610). The best-fit evolution model for BI was "GTR+I+G." The average standard deviation of split frequencies was 0.009192. The topologies of trees obtained from ML, MP, and BI were almost the same. Only the ML tree is shown in FIG. 1, with maximum

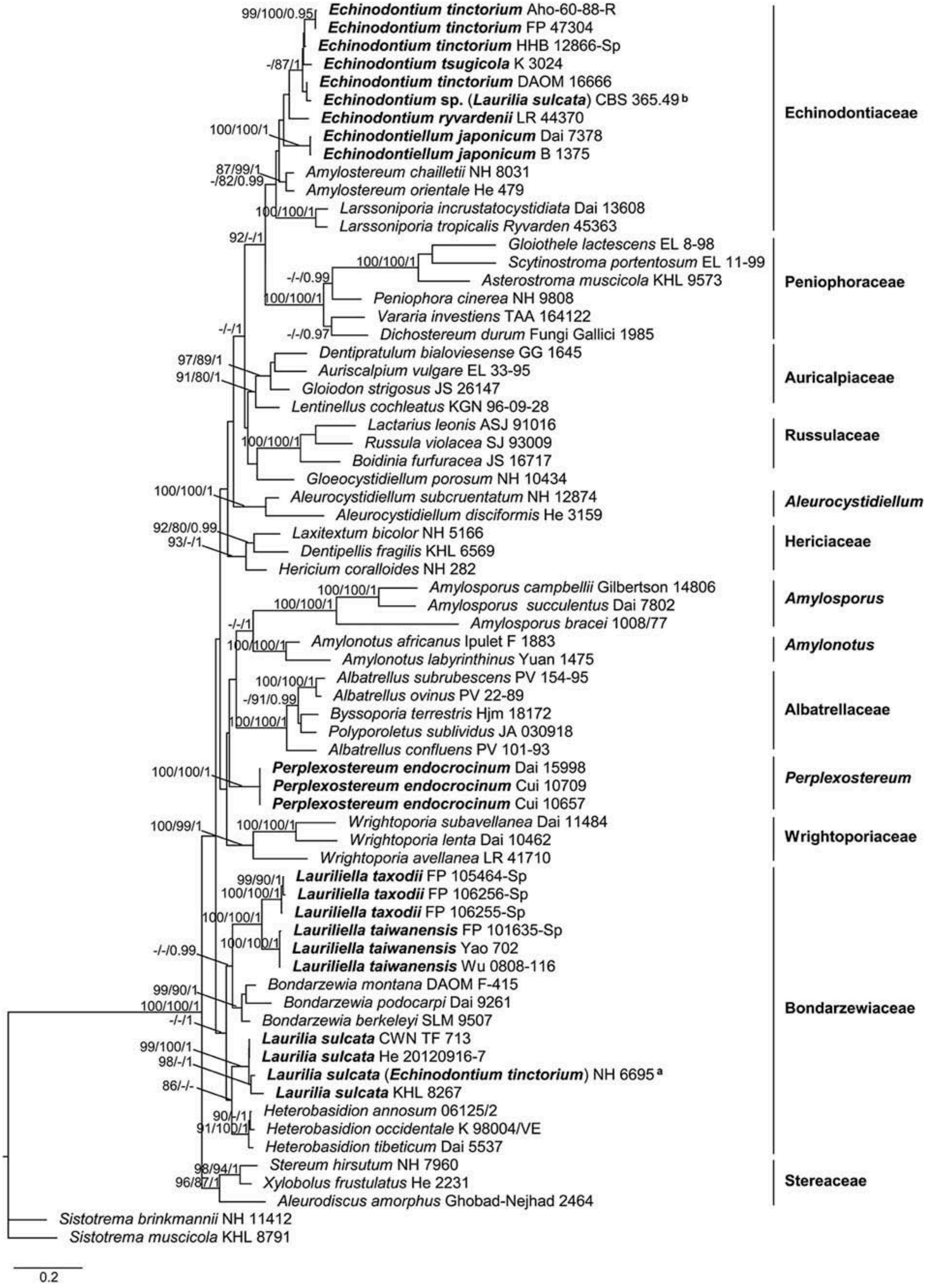

Figure 1. Phylogenetic tree inferred from maximum likelihood (ML) analysis based on a concatenated data set of ITS and 28S sequences data of taxa in Russulales. Branches are labeled with maximum likelihood and maximum parsimony bootstrap values ≥80%, and Bayesian posterior probabilities ≥0.95. [a]The sequence labeled *Echinodontium tinctorium* (NH 6695, AF506430) by Larsson and Larsson (2003) clustered with *Laurilia sulcata*. [b]The sequence labeled *Laurilia sulcata* (CBS 365.49, AF518626) by Hibbett and Binder (2002) clustered with *Echinodontium* species.

likelihood bootstraps (LB) and maximum parsimony bootstraps (PB) ≥80% and Bayesian posterior probabilities (PP) ≥0.95 labeled along the branches. In the tree, *Amylostereum, Echinodontiellum, Echinodontium*, and *Larssoniporia* Y.C. Dai, Jia J. Chen & B.K. Cui are included in the Echinodontiaceae, whereas *Bondarzewia, Heterobasidion, Laurilia*, and *Lauriliella* are in the Bondarzewiaceae. *Perplexostereum* forms a distinct clade from the Echinodontiaceae and Bondarzewiaceae. *Echinodontium* sensu stricto (s.s.) includes three taxa: *E. tinctorium, E. tsugicola*, and *E. ryvardenii* (FIG. 1).

TAXONOMY

Echinodontiellum S.H. He & Nakasone, gen. nov.
MycoBank MB819204

Typification: Echinodontium japonicum Imazeki, J Jap Bot 11:520. 1935.

Etymology: Diminutive of *Echinodontium*.

Genus diagnosis: Basidiocarps perennial, resupinate to slightly effused-reflexed, woody hard. Hymenophore dentate, gray to olive gray. Teeth scattered to dense, conical, rigid, brittle. Margin determined, velvety, narrow. Subiculum cinnamon or olive gray to brownish gray, woody hard, darkening in KOH. Hyphal system dimitic. Generative hyphae thin- to thick-walled, hyaline, nodose-sepatate, with scattered secondary simple septa. Skeletal hyphae thick-walled to subsolid, light brown. Cystidia numerous, clavate, hyaline to light brown, thick-walled, apically encrusted, blunt, embedded or slightly projected. Basidia clavate, hyaline, with 4 sterigmata and a basal clamp connection. Basidiospores ellipsoid, hyaline, thick-walled, echinulate, amyloid. Causing a white rot on living *Quercus* in Japan and China.

Notes: The morphological differences between *Echinodontium* and *Echinodontiellum* are small but significant. Basidiocarps of *Echinodontiellum* are effused to effused-reflexed, whereas they are effused-reflexed to pileate, rarely effused, in *Echinodontium*. The context in *Echinodontiellum* is cinnamon to olive gray or brownish gray that darkens in KOH. In comparison, the context in *Echinodontium* species are brick red or brownish orange that turns maroon in KOH or pale brown to brown (in *E. ryvardenii*). No significant microscopic differences between the genera were observed. Sequence differences between *Echinodontium tinctorium* and *Echinodontiellum japonicum* were 14.7% of 543 base pairs in the ITS region and 2.3% of 1330 base pairs in the 28S region. These values are comparable to that observed between *Laurilia sulcata* and *Heterobasidion annosum* (Fr.) Bref.: 14.2% of 555 base pairs and 2.4% of 1350 base pairs, respectively. Finally, *Echinodontiellum* occurs exclusively on *Quercus*, whereas *Echinodontium* s.s. prefers gymnospermous substrates.

Echinodontiellum japonicum (Imazeki) S.H. He & Nakasone, comb. nov. FIG. 2A
MycoBank MB819209

Basionym: Echinodontium japonicum Imazeki, J Jap Bot 11:520. 1935.

For descriptions, see Imazeki (1935), Gross (1964), Hattori and Ryvarden (1994), and Núñez and Ryvarden (2001). This is an uncommon species found on *Quercus*.

Specimen examined: CHINA. FUJIAN: Wuyishan Co., Wuyishan Nature Reserve, Taoyuanyu, on fallen trunk of *Quercus*, 22 Oct 2005, *Dai 7378* (BJFC 016582).

Lauriliella S.H. He & Nakasone, gen. nov.
MycoBank MB819211

Typification: Stereum taxodii Lentz & H.H. McKay, Mycologia 52:262. 1961 [1960].

Etymology: Diminutive of *Laurilia*, a name to honor the Finnish mycologist Matti Laurila, who published from 1915 to 1942.

Genus diagnosis: Basidiocarps perennial, effused-reflexed, pileate or umbonate, woody hard. Upper surface velutinous, grayish brown to dark brown, sulcate, becoming glabrous, black, rimosus with age; margin acute to blunt, thickening with age. Hymenophore smooth to tuberculate, grayish orange, brownish orange to light brown; margin sterile, distinct. Context brownish orange to light brown, woody hard. Hyphal system dimitic. Generative hyphae thin- to thick-walled, hyaline, nodose-septate, with scattered secondary simple septa. Skeletal hyphae dominant, thick-walled to subsolid, light yellow, unbranched. Cystidia hyphoid to clavate, thick-walled, apically encrusted, embedded or slightly projected. Basidia clavate, hyaline, with 4 sterigmata and a basal clamp connection. Basidiospores broadly ellipsoid to subglobose, hyaline, thick-walled, echinulate, amyloid. Associated with white stringy rot to brown powdery rot in pockets, often associated with living trees of Cupressaceae.

Notes: With the transfer of *Laurilia taxodii* to *Lauriliella, Laurilia* becomes monotypic. Although similar, *Laurilia* and *Lauriliella* can be distinguished by several critical features. *Laurilia* causes a white stringy rot or white pocket rot of dead coniferous wood, whereas *Lauriliella* creates large pockets of decayed wood scattered in heartwood of *Taxodium* and *Chamaecyparis* that is somewhat stringy or laminated. The hymenophore is light yellow or pink to salmon-colored in *Laurilia* but gray, orange, or brown in *Lauriliella*. Microscopically, unbranched skeletal hyphae are dominant in the context of *Lauriliella*,

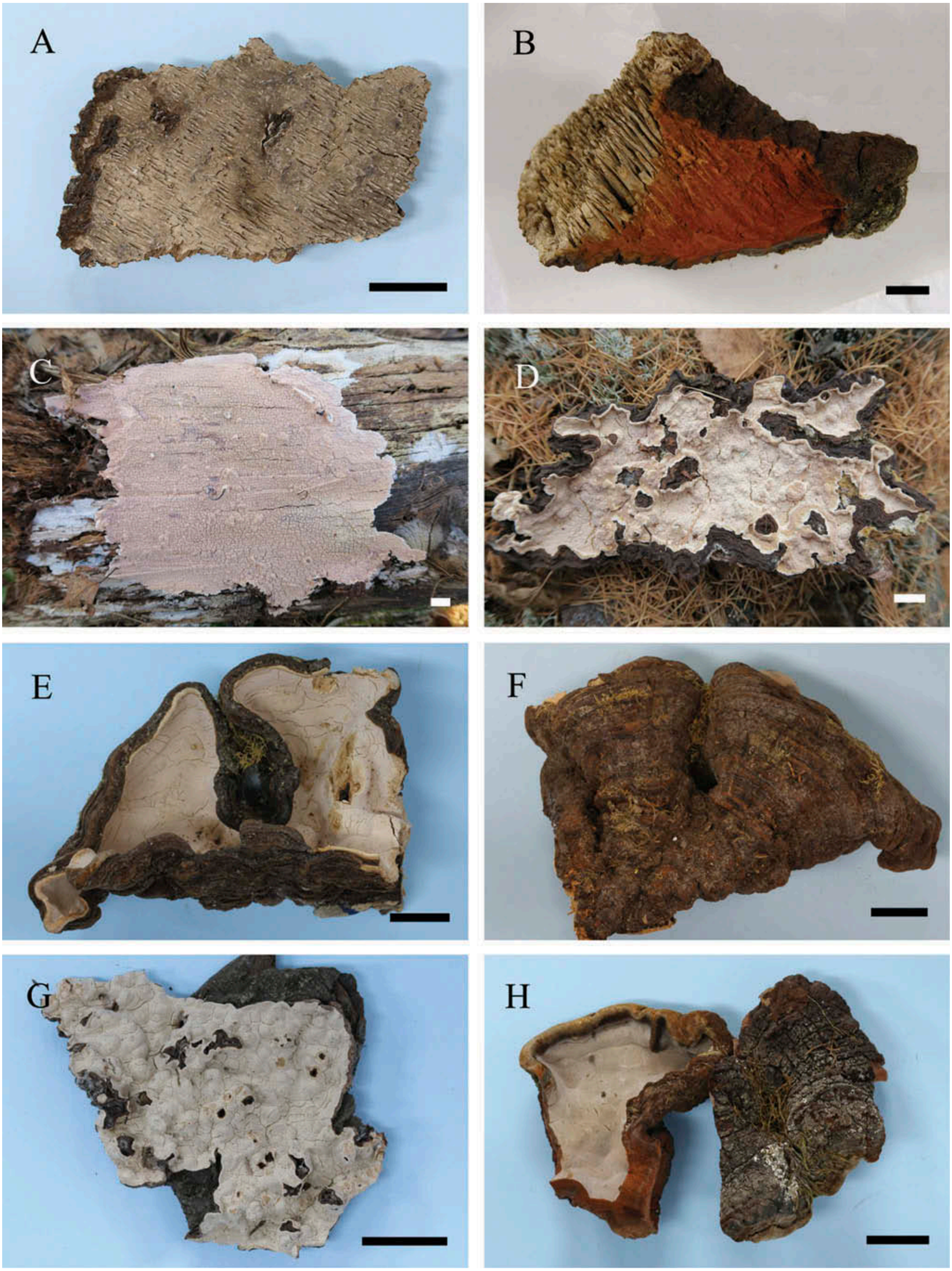

Figure 2. Basidiocarps of *Echinodontiellum, Echinodontium, Laurilia, Lauriliella*, and *Perplexostereum*. A. *Echinodontiellum japonicum* (Dai 7378). B. *Echinodontium tinctorium* (HHB 12866-Sp). C–D. *Laurilia sulcata* (C: He 2999; D: He 3026). E–F. *Lauriliella taiwanensis* (holotype, FP-10635). G. *Lauriliella taxodii* (FP-105464-Sp). H. *Perplexostereum endocrocinum* (Dai 4219). All scale bars equal 1 cm.

whereas in *Laurilia* unbranched skeletals and richly branched binding hyphae are present. Davidson et al. (1960) and Nakasone (1990) noted differences in cultures, with *Laurilia sulcata* growing faster, producing strong oxidase reactions, and developing conidia (*Spiniger* anamorph). In contrast, *Lauriliella taxodii* cultures grew very slowly and produced no or weak oxidase reactions and produced chlamydospores.

Lauriliella taxodii (Lentz & H.H. McKay) S.H. He & Nakasone, comb. nov. FIG. 2G
MycoBank MB819213

Basionym: Stereum taxodii Lentz & H.H. McKay, Mycologia 52:262. 1961 [1960].

See Davidson et al. (1960) and Gross (1964) for descriptions of basidiocarps and Davidson et al. (1960) and Nakasone (1990) for cultural descriptions.

Specimens examined: USA. MISSISSIPPI: Bolivar Co., on living *Taxodium distichum*, 28 Oct 1959, *FP-106253* (CFMR) and *FP-106256* (CFMR); 2 Dec 1959, *FP-105464* (CFMR).

Lauriliella taiwanensis S.H. He & Nakasone, sp. nov. FIGS. 2E–F, 3
MycoBank MB819216

Typification: CHINA. TAIWAN: Kaohsiung, Ah-Kuo, on *Chamaecyparis formosensis*, 25 Jan 1975, *FP-101635* (**holotype** in CFMR).

Etymology: Referring to the type locality.

Fruiting body: Basidiocarps perennial, pileate, umbonate to almost cupulate, attached to substrate by an umbonate point, becoming bell-shaped, attached to substrate by a broad side with age, woody hard. Pileus projecting up to 5 cm, 12 cm wide and 4 cm thick at center. Pileal surface brown [6E(4–8)] to dark brown [6F(4–8)], concentrically sulcate and zonate, velutinous, becoming dark brown to almost black, deeply and densely cracked from the basal part with age; margin blunt, usually with hymenophore effused over, thickening with age, up to 0.4 cm thick. Hymenophore smooth, light orange [6A(4–5)], grayish orange [6B(3–6)], brownish orange [6C(3–8)] to light brown [6D(4–8)], cracked with age; sterile margin slightly darker colored than hymenophore surface, distinct, up to 0.3 cm wide. Context light orange to light brown, woody hard, up to 0.2 cm thick. Subhymenium thickening with age, concolorous with context.

Hyphal system dimitic; generative hyphae nodose-septate. Tissue unchanged in KOH.

Context: Hyphae densely interwoven, more or less regularly arranged. Generative hyphae frequent, hyaline, thin- to slightly thick-walled, occasionally branched, frequently septate, 2.5–5 µm in diam. Skeletal hyphae dominant, light yellow to yellow, distinctly thick-walled to subsolid, unbranched, straight, with scattered secondary simple septa, 3–6 µm in diam.

Subhymenium: Hyphae vertically arranged, densely interwoven and agglutinated, with embedded basidiospores. Generative hyphae frequent, hyaline, thin- to thick-walled, occasionally branched, frequently septate, 3–6 µm in diam. Skeletal hyphae hyaline to light yellow, thick-walled to subsolid, unbranched, 4–7 µm in diam. Cystidia frequent, hyphoid to clavate, distinctly thick-walled, apically encrusted, 5–8 µm wide (encrustation excluded).

Hymenium: Cystidia similar to those in subhymenium, frequent, not or slightly projected. Basidia clavate, hyaline, thin-walled, with four sterigmata and a basal clamp connection, 65–90 × 5–8 µm; basidioles similar to basidia, numerous. Basidiospores broadly ellipsoid to subglobose, hyaline, thick-walled, echinulate, bearing a small apiculus, strongly amyloid, 6–8 × (5–)5.5–7(–7.5) µm, L = 6.9 µm, W = 6 µm, Q = 1.13–1.17 (n = 90/3).

Habitat: On living *Chamaecyparis formosensis* in Taiwan.

Notes: Lauriliella taiwanensis was reported as *Laurilia taxodii* (*Stereum taxodii*) from Taiwan (Aoshima et al. 1961; Gross 1964; Davidson and Chien 1976). However, molecular evidence and morphological examination reveal that they are distinct species. In FIG. 1, *L. taiwanensis* and *L. taxodii* formed distinct, sister lineages with high support values. Morphologically, *L. taiwanensis* differs from *L. taxodii* in having larger and tougher, umbonate to bell-shaped basidiocarps. Moreover, *L. taiwanensis* is found in Taiwan on *Chamaecyparis*, whereas *L. taxodii* is found in southeastern United States on *Taxodium*. Interestingly, Davidson and Chien (1976) reported that single-spore isolates of *L. taxodii* (= *L. taiwanensis*) from Taiwan were interfertile with those from *L. taxodii* from Mississippi, USA. Reports of *L. taxodii* from Japan on *Torreya* and *Cryptomeria* (Aoshima et al. 1961; Gross 1964) need to be verified. BLAST search shows that the ITS sequence of *Echinodontium taxodii* (AF218402) in Tabata et al. (2000) is from a contaminating *Phlebia* sp.

Other specimens examined: CHINA. TAIWAN: Taichung Co., Hoping Hsiang, on fallen trunk of angiosperm?, 20 Aug 2008, *Wu 0808-116* (F0022738); Alishan, Chiayi Ran-dai Mountains, on *Chamaecyparis formosensis*, 16 Sep 1974, *FP-101645* (CFMR); Balon, Tau-Yuan, on *Chamaecyparis formosensis*, 2 Jan 1975, *FP-101626* (CFMR); Nantou Co., Lugu Hsiang, Sitou, 120°47′55″E, 23°39′39″N, alt. 1320 m, on trunk of *Chamaecyparis formosensis*, Oct 2016, *Yao 7025* (TNM).

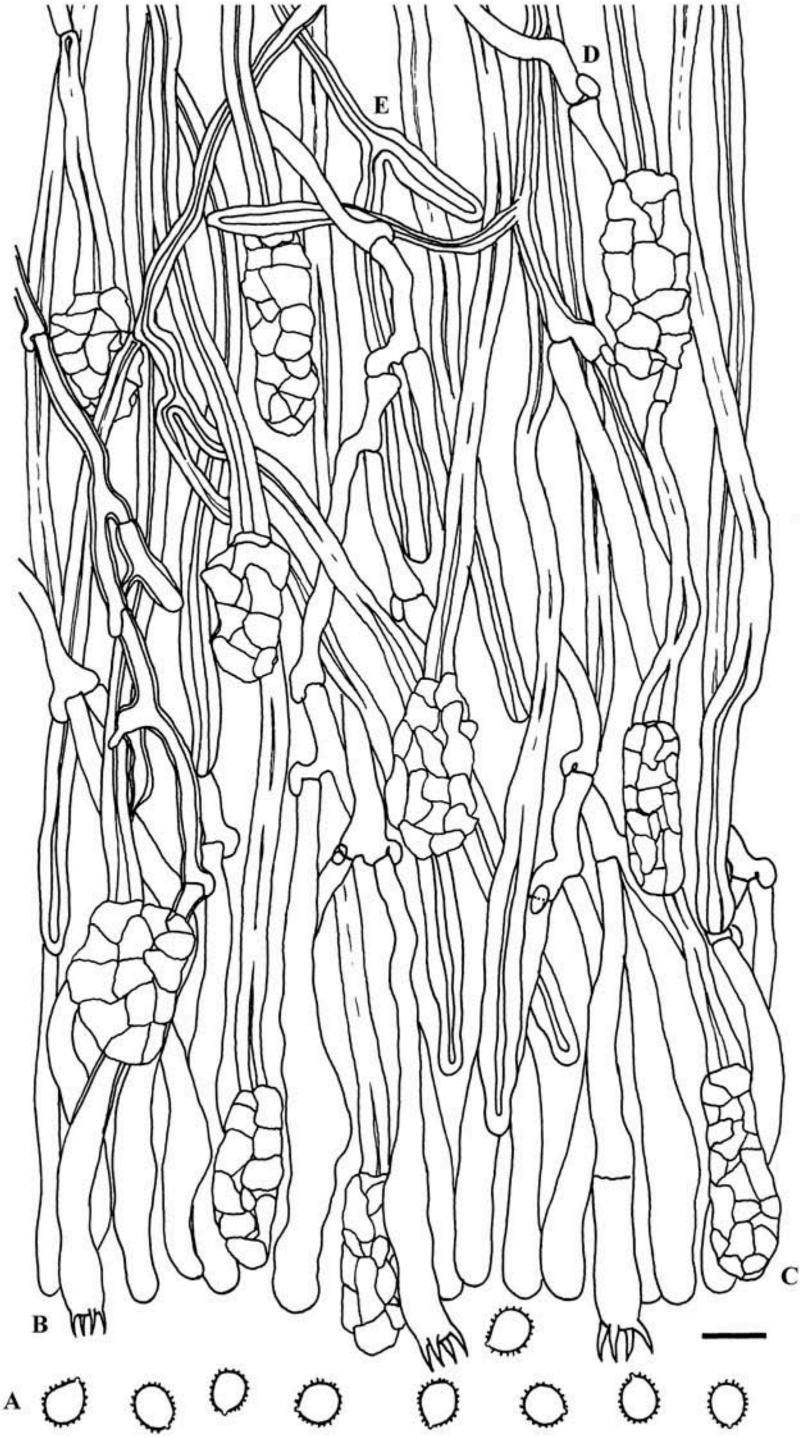

Figure 3. A cross-section of hymenium and subhymenium of *Lauriliella taiwanensis* (drawn from holotype, FP-10635). A. Basidiospores. B. Basidia. C. Cystidia. D. Generative hyphae. E. Skeletal hyphae. Scale bar = 10 µm.

DISCUSSION

Nine species of *Echinodontium* and allied, nonporoid genera are known (Gross 1964; Bernicchia and Piga 1998; Ryvarden and Tutka 2014). Except for *E. ballouii* (Banker) H.L. Gross, a rare species known only from New Jersey, USA, eight species were included in our phylogenetic analyses. In FIG. 1, the Echinodontiaceae clade includes four species with dentate hymenophores, *Echinodontium tinctorium* (FIG. 2B), *E. tsugicola* (Henn. & Shirai) Imazeki, *E. ryvardenii*, and *Echinodontiellum japonicum*, as well as *Amylostereum* (smooth hymenophore) and *Larssoniporia* (poroid hymenophore). The four remaining species have smooth to tuberculate hymenophores. Whereas *Laurilia sulcata* (FIG. 2C–D), *Lauriliella taiwanensis*, and *Lauriliella taxodii* cluster with *Bondarzewia* and *Heterobasidion* (both with poroid hymenophores), *Perplexostereum endocrocinum* (FIG. 2H) forms a distinct clade. For family and clade names, Echinodontiaceae (Donk 1961) has priority over Amylostereaceae (Boidin et al. 1998), whereas Bondarzewiaceae (Kotlaba and Pouzar 1957) is available for the *Laurilia*/*Heterobasidion* group.

Our analyses also recovered *Echinodontium tinctorium* (generic type) as closely related to *Amylostereum*, as it was shown by previous studies (Tabata et al. 2000; Hibbett and Binder 2002; Binder et al. 2005) (FIG. 1). *Echinodontium tinctorium*, *E. tsugicola*, and *E. ryvardenii* are considered to be *Echinodontium* s.s. *Echinodontiellum japonicum* is sister to *Echinodontium* s.s. and segregated into a separate genus because of the ecological, basidiocarp, and molecular criteria. This rare species was originally described in Japan and is here recorded for the first time in China. It grows exclusively on *Quercus*, whereas species of *Echinodontium* s.s. and *Amylostereum* associate with gymnospermous substrates. Morphologically, *Echinodontiellum japonicum* has resupinate to effused-reflexed basidiocarps with a distinct olive color in the hymenophore.

Echinodontium ryvardenii is considered to be a true *Echinodontium* but is also a conundrum, and its relationship to *Echinodontium* and *Echinodontiellum* is unclear. For example, its basidiocarp morphology encompasses the range observed in *Echinodontium* and *Echinodontiellum*, from pileate to effused, but with a pale brown to brown context that is not found in either genus. It occurs exclusively on *Juniperus* in southern Europe. In phylogenetic studies, its position varies widely—far removed from *E. tinctorium* and *L. sulcata* (Larsson and Larsson 2003; Miller et al. 2006; Chen et al. 2016) or in the same clade with other *Echinodontium* species (FIG. 1).

Previously, Larsson and Larsson (2003) and Miller et al. (2006) showed that *E. tinctorium* clustered with *Bondarzewia* and *Heterobasidion*. Our phylogenetic analyses, however, indicate that the sequence of *E. tinctorium* (AF506430, NH 6695) used in these papers is actually a sequence of *Laurilia sulcata*. The voucher specimen should be examined to confirm this.

Although *Lauriliella taxodii* and *Laurilia sulcata* are often placed in the same genus (Chamuris 1988; Ginns and Lefebvre 1993; Stalpers 1996), our results show that they are distinct genera (FIG. 1). *Laurilia sulcata* (generic type), widely distributed in the boreal conifer forest in north hemisphere, is sister to *Heterobasidion*, whereas *Lauriliella taxodii* and *L. taiwanensis* formed a distinct group sister to *Bondarzewia* (FIG. 1). In addition to sequence differences, *Lauriliella* and *Laurilia* can be distinguished on morphological and ecological features. *Laurilia sulcata* has a trimitic hyphal system with branched binding hyphae and prefers dead limbs and trunks of the Pinaceae, whereas species of *Lauriliella* have a dimitic hyphal system and inhabits living trees of the Cupressaceae. *Laurilia*, *Heterobasidion*, and *Bondarzewia* species produce a *Spiniger* anamorph in culture (Stalpers 1996), whereas chlamydospores, not conidia, are produced in *Lauriliella* (as *L. taxodii*; Davidson et al. 1960). *Laurilia* is now monotypic with the transfer of *L. taxodii* to *Lauriliella*. The sequence labeled *Laurilia sulcata* (AF518626, CBS 365.49) by Hibbett and Binder (2002) is probably based on an *Echinodontium* species as shown in FIG. 1. The voucher specimen (FP-71688-R) at CFMR was examined and confirmed to be *L. sulcata*, so the culture is probably a contaminant of *Echinodontium*. Because *Echinodontium* produces conidia, this is likely the source of the contamination.

Perplexostereum endocrocinum, originally described from Nepal, is new to China and is presumed to be widely distributed in the high-altitude areas in southwestern China on the Cupressaceae. It is characterized by pileate basidiocarps, a smooth hymenophore, a dimitic hyphal system, long smooth gloeocystidia, and ornamented, amyloid, subglobose basidiospores (Ryvarden and Tutka 2014). The ITS sequences of the Chinese specimens are identical with that from a Nepalese specimen (pers. comm. from Leif Ryvarden). In the phylogenetic analyses (FIG. 1), *P. endocrocinum* forms a distinct clade from the Bondarzewiaceae and Echinodontiaceae.

Based on our analyses, only *Laurilia sulcata* seems to have a wide distribution, whereas others are restricted to some specific areas and substrates. This is partially because of insufficient collecting, but more importantly, many of these taxa have strong host preferences with living trees.

KEY TO GENERA IN THE ECHINODONTIACEAE AND BONDARZEWIACEAE AND SPECIES OF *ECHINODONTIELLUM, ECHINODONTIUM, LAURILIA, LAURILIELLA,* AND *PERPLEXOSTEREUM*

1. Hymenophore poroid..2

1′. Hymenophore nonporoid.. 4

2. Basidiospores nonamyloid....................*Heterobasidion*

2′. Basidiospores amyloid.. 3

3. Dextrinoid skeletoid hyphae absent; cystidia smooth .... *Bondarzewia*

3′. Dextrinoid skeletoid hyphae present; cystidia encrusted .... *Larssoniporia*

4. Basidiospores smooth........ *Amylostereum*

4′. Basidiospores ornamented 5

5. On angiosperms .... *Echinodontiellum japonicum*

5′. On gymnosperms........ 6

6. Hymenophore dentate to daedaleoid or poroid 7

6′. Hymenophore smooth or tuberculate........ 10

7. Context brick red........ 8

7′. Context brown........ 9

8. Basidiocarps pileate to ungulate; known from western North America........ *Echinodontium tinctorium*

8′. Basidiocarps effused-reflexed to pileate; known from Japan........ *Echinodontium tsugicola*

9. Context with a dark line; on *Juniperus* in Europe........ *Echinodontium ryvardenii*

9′. Context without a dark line; on *Chamaecyparis* in eastern United States........ *Echinodontium ballouii*

10. Basidiocarps resupinate to effuse-reflexed; hyphal system trimitic; associated with dead Pinaceae, cosmopolitan species .... *Laurilia sulcata*

10′. Basidiocarps pileate; hyphal system dimitic; associated with living Cupressaceae, locally distributed species 11

11. Context reddish brown; cystidia smooth; known from southwestern China and Nepal.... *Perplexostereum endocrocinum*

11′. Context light orange to light brown; cystidia encrusted; known from elsewhere 12

12. Basidiocarps resupinate to effuse-reflexed; on *Taxodium* in southeastern United States *Lauriliella taxodii*

12′. Basidiocarps pileate; on *Chamaecyparis* in Taiwan .... *Lauriliella taiwanensis*

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