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Calicium sequoiae, a new lichen species from north-western California, USA

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Abstract: We describe *Calicium sequoiae* as a new species of lichenized Ascomycota from north-western California, USA. The species is distinguished morphologically from other known members of *Calicium* by its stalks that react I+ blue, mature ascospores that are ornamented with spiral ridges, and apothecia that produce prominent white pruina. It is also the only *Calicium* known to produce thamnolic acid as a major secondary substance. Sequences from the ITS-region showed *C. sequoiae* to be unique among calicioid *Physciaceae*, and phylogenetic analysis positioned it close to *C. adspersum*, *C. chlorosporum*, *C. lenticulare*, *Cyphelium notarisii*, and *C. tigillare*. Thus far, *Calicium sequoiae* has been collected only from old-growth redwood (*Sequoia sempervirens*) forests, where it occurred on thick, fibrous bark of large redwood trees. A key to the 12 species of *Calicium* known from the Pacific Northwest is provided.

Key words: Ascomycota, California, *Caliciaceae*, calicioid, key, Pacific Northwest, *Physciaceae*, redwood, *Sequoia sempervirens*

Introduction

Calicioid lichens and fungi are characterized by evanescent asci that form a mazaedium of passively dispersed spores. New species have been described recently from Africa and Madagascar (Tibell 2000), Europe (Tibell 1996, 1999*a*), India (Tibell 2006), Japan (Tibell & Thor 2003), Australasia (Tibell 1983, 1987), eastern Russia (Titov & Tibell 1993; Tibell & Titov 1995), South America (Tibell 1998), Costa Rica (Tibell 1982), and North America (Peterson & Rikkinen 1998; Rikkinen 1999, 2003*a*, *b*; Selva & Tibell 1999; Tibell & Koffman 2002). This '*Caliciales*' assemblage, once considered a paragon of monophyly united by mazaedia, has turned out to be suspiciously polyphyletic (Tibell 1984) and was ultimately rendered superfluous by phylogenetic analyses (Gargas & Taylor 1995; Wedin & Tibell 1997). Moreover, the core group within the '*Caliciales*' that appeared to be monophyletic (i.e., *Caliciaceae*, *Mycocaliciacae*, and *Sphinctrinaceae*) was instead confirmed to be polyphyletic (Wedin & Tibell 1997). Further systematic scrutiny placed the *Caliciaceae* within the *Physciaceae* (Wedin *et al*. 2002; Helms *et al*. 2003; Miądlikowska *et al.* 2007), and a proposal to abandon the family name *Caliciaceae* while conserving *Physciaceae* has been presented (Wedin & Grube 2002). Even *Calicium*, the nucleus of the former *Caliciaceae*, was determined to be paraphyletic with respect to *Acroscyphus*, *Texosporium*, *Tholurna*, and several species of *Cyphelium* (Tibell 2006).

Despite the systematic demotion of the '*Caliciales*' into artificiality, lichenologists have benefited from the assemblage's ecological fastidiousness. Relationships between many calicioids and old forests have been revealed (Holien 1996; Dettki *et al*. 1998; Kuusinen & Siitonen 1998; Peterson 2000; Rikkinen 2003*c*). Some have even been used to evaluate forest age, continuity, and conservation (Tibell 1992; Selva 1994;

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USDA & USDI 1994). Old-growth forests in the Pacific Northwest of North America support an exceptionally rich mycota of calicioid lichens and fungi (Peterson 2000; Rikkinen 2003*c*). This richness almost certainly results from the relative abundance of intact forests containing a high diversity of endemic tree species compared to other regions. Several of these calicioid species are narrow endemics that specialize on just a few host tree species (Bonar 1971; Tibell 1991; Tibell & Titov 1995; Rikkinen 1999, 2003*a*,*b*). *Mycocalicium sequoiae* Bonar, for example, exclusively occupies resin of *Sequoiadendron giganteum* (Lindl.) Buchh. (Giant Sequoia) and *Sequoia sempervirens* (D. Don) Endl. (Redwood).

Old-growth redwood forests contribute substantially to the calicioid mycota of the Pacific Northwest. Calicioid lichens and fungi near the ground are more diverse in these forests than in other mixed conifer-hardwood forests nearby, and tree bases and fallen logs are important substrata for this assemblage (Rikkinen 2003*c*). Canopies of old-growth redwood forests also support a rich array of calicioids, especially the lichenized genera *Calicium* and *Chaenotheca* that occur well above the forest floor on moderately sheltered, stable substrata such as bare wood and old bark (Williams & Sillett 2007). In these forests, several large redwoods supported a previously undescribed species of *Calicium* that may be endemic to old-growth redwood forests. We describe this new species, place it among the calicioid *Physciaceae*, and provide an updated identification key to *Calicium* from the Pacific Northwest.

Material and Methods

Specimens were collected by C. Williams as part of a larger project that investigated epiphyte communities on redwood in north-western California (*Calicium* sp. nov.; Williams & Sillett 2007). Separate collections were defined as material either occurring on separate individual trees, or if occurring on the same tree, then at least 5 m apart. Morphological features were measured by light microscopy of the material mounted in water. We performed morphometric analyses to obtain estimated values of apothecium height, capitulum diameter, excipulum and hypothecium thicknesses, ascus length and diameter, and ascospore size. The results are presented as follows: '(min)a–b(max)', where 'a' is the mean minus 1·0 standard deviation, 'b' is the mean plus 1·0 standard deviation, '–' indicates the range between 'a' and 'b', and finally 'min' and 'max' denote the minimum and maximum recorded values, respectively. Estimated values are followed by the sample size (*n*). Detailed ornamentation of the ascospore was studied with scanning electron micrography using air-dried, gold-coated material mounted to specimen stubs.

To determine the position of *Calicium sequoiae* among the calicioid *Physiaceae*, we took advantage of a recent portrayal of phylogenetic relationships within *Calicium* (Tibell 2006). Therefore, our phylogenetic methods, including isolation, PCR-amplification of the nuclear rDNA ITS1-5.8S-ITS2, sequencing, choice of outgroup, and analysis used to elucidate phylogenetic relationships were performed as indicated in that work. The ITS-sequences from three specimens of *C. sequoiae* were compared with 65 additional sequences representing 29 calicioid lichen species within the *Physciaceae* plus *Diplotomma alboatrum* (Hoffm.) Flot. as an outgroup; a total of 69 sequences from 31 species [i.e. the matrix used in Tibell (2006) with the addition of *C. sequoiae*].

The Species

Calicium sequoiae Williams & Tibell sp. nov.

Thallus flavidus vel viridulus, bene evolutus granulosus vel immersus, K+ fulvus, C − , KC − , Pd+ aurantiacus, UV − , acidum thamnolicum continens. Algae *Trebouxiae* similes. Apothecia 0·52–0·94 mm alta, pruina distincta alba in pagina externa excipuli. Capitula 0·23–0·42 mm diametro lenticularia ad globosa vel obconica. Asci evanescentes, clavati, 19·4–21·8 × 5·8–7·5 µm, octospori, sporis biseriate ad triseriate ordinatis. Sporae parvae, 8·5–11·0 × 3·4–4·4 µm, ubi juvenes et maturae ornamento spirali valde distincto, in sporis veteribus a rimis irregularibus disrupto. Stipes 0·07–0·14 mm diametro, I+ caeruleus ad purpureus.

Typus: USA, California, Humboldt County, Prairie Creek Redwoods State Park, 430 m north-east of Cal Barrel Road's intersection with Newton B. Drury Scenic Parkway, 41°22′15″N, 124°0′48″W, alt. 55 m, in an old-growth redwood forest. On bark of large *Sequoia sempervirens* at 30 m above ground, January 2007, *Cameron B. Williams* 1299 (UPS—holotypus).

(Fig. 1)

Thallus crustose, episubstratic to rarely partly endosubstratic; pale yellow to yellowish green or occasionally green, dull; granular, in poorly developed thalli the granules frequently exploiting open microinterstices

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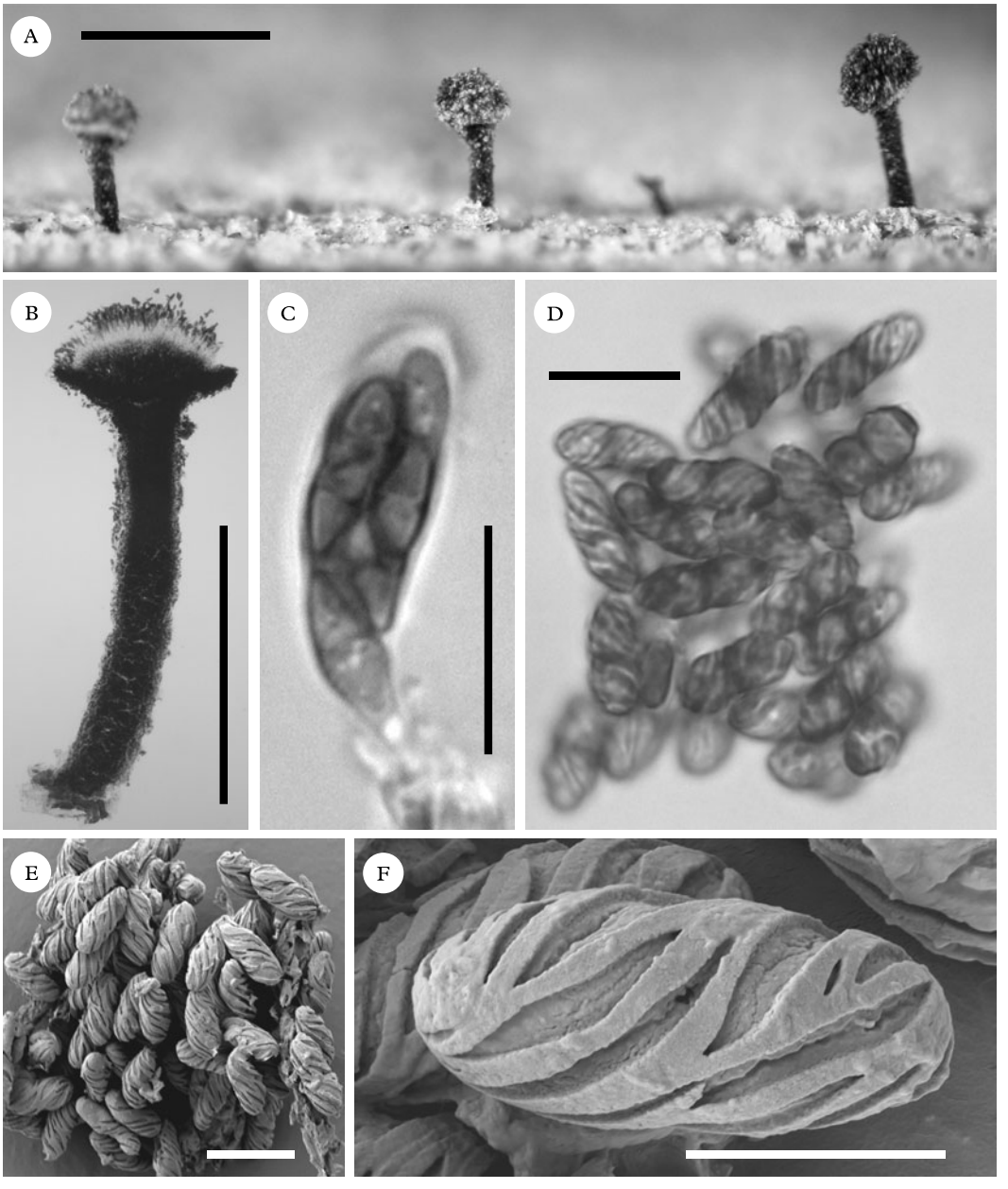

FIG. 1. *Calicium sequoiae.* A, granular thallus supporting three mature apothecia with spherical capitula, each displaying a white pruina most prominent around rim of excipulum; B, median longitudinal section through mature apothecium with a broadly obconical capitulum and heavily sclerotized excipulum (LM); C, maturing clavate ascus holding young, weakly ornamented, 2-celled ascospores that are biseriately arranged and longitudinally oriented (LM); D, cluster of liberated, mature ascospores exhibiting translucent medium grey colour, septa constrictions, and prominent spiral ornamentations (LM); E, mature ascospores each ornamented with a network of left-handed spiral ridges that converge at the spore apices (SEM); F, single ascospore detailing the surface texture of ridges and troughs that form a network of spirals (SEM). Scales: A=1mm, B=0·5mm; C–E=10 μm; F=5 μm.

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of the substratum, and in well-developed thalli the granules coalescing into individual masses separated by cracks that give an overall tessellate appearance. *Photobiont* trebouxioid.

Apothecia black, stalked, mazaediate, (0·35)0·52–0·94(1·13) mm tall (n=25); pruina white, most prominent around rim of excipulum, typically dusting mazaedium, coating lower surface of excipulum, and diminishing downwards along stalk. Decrepit apothecia usually develop a hyperabundant pruina. *Capitulum* broadly lenticular to hemispherical or spherical, occasionally obconical, (0·18)0·23–0·42 (0·49) mm diam. (n=25). *Excipulum* dark brown, (20)24–50(60) µm thick (measured at base of hypothecium; n=16); consisting of slightly elongate, heavily sclerotized, anticlinally arranged hyphae that become shorter and more sclerotized toward the margin. *Hypothecium* medium to dark brown with a convex upper surface, (30)31–45 (51) µm thick (measured above centre of stalk; n=16); consisting of periclinally arranged, moderately sclerotized, somewhat interwoven hyphae. *Asci* evanescent, clavate, (17·6)19·4–21·8(28·0) µm long (n=25), (4·8)5·8–7·5(8·0) µm diam. (n=25); each containing eight bi- to triseriately arranged, longitudinally to somewhat obliquely oriented ascospores. *Ascospores* translucently grey to greyish brown, 2-celled, (6·8)8·5–11·0(12·8) µm long (n=80), (3·0)3·4–4·4(4·8) µm diam. (n=25); ornamented with a network of prominent, left-handed spiral ridges that converge at the spore apices. Young spores develop a light grey colour, septa, and weak spiral ridges within the ascus, then are discharged and mature with a medium grey colour, septa constrictions, and prominent spirals, and finally turning a greyish brown colour with occasional irregular cracks disrupting the spiral ridges. *Stalk* black, dull, sometimes slightly swollen at the base, (0·05)0·07–0·14(0·21) mm diameter (n=25); constructed of heavily sclerotized, interwoven hyphae that are slightly paler toward the outside of the stalk.

Conidiomata not observed.

Chemistry. A thallus fragment subjected to high performance liquid chromatography revealed thamnolic acid as a major secondary substance as well as decarboxythamnolic acid, protocetraric acid, and squamatic acid in minor or trace amounts (J. Elix, pers. comm.). Thus, the thallus reacts K+ yellow and Pd+ orange, but C−, KC−, and UV−. The stalk contains starches that react I+ blue or sometimes weakly bluish purple.

Etymology. The specific epithet was derived from the monotypic genus *Sequoia* (redwood). *Calicium sequoiae* has been collected only from large redwood trees in old-growth redwood forests, a habitat to which it may be endemic. We offer the common name 'redwood stubble'.

Phylogenetic relationships. The three sequences from *C. sequoiae* clustered together with high support (Fig. 2), and the ITS region contained unique sequence fragments (i.e., CGTCGGTCGGGGCGGCA in ITS1 and GGCGGTCCGCCGGGACT plus CGGCCAACTCTCCATGA in ITS2) that distinguished it from other calicioid *Physciaceae*. *Calicium sequoiae* belongs to 'Clade II' of Tibell (2006) which also contains *C. adspersum* Pers., *C. chlorosporum* F. Wilson, *C. lenticulare* Ach., *Cyphelium notarisii* (Tul.) Blomb. & Forss., and *Cy. tigillare* (Ach.) Ach., but it does not include the type of the genus *Calicium viride* Pers.

Distribution. Specimens were collected from north-western California in Humboldt Redwoods State Park, Redwood National Park, Prairie Creek Redwoods State Park, and Six Rivers National Forest, where they ranged from 40·3° to 41·5°N latitude and 3 to 37 km from the Pacific Ocean.

Ecology. Numerous large (>0·25 m^2) occurrences were observed on thick, fibrous bark between 20 and 80 m above ground level on trunks of large redwood trees in low elevation, old-growth redwood forests growing on flood plains of major creeks. The crown structure of the host trees provided a

relatively dry, shady, stable, protected microhabitat.

Specimens examined. **USA:** *California*: Del Norte County, Six Rivers National Forest: west bank of High Prairie Creek, 41°34′46″N, 124°3′55″W, 50 m above ground, 2008, *Williams* 1301 (HSC); Humboldt County, Prairie Creek Redwoods State Park, 5·1 km north of Cal Barrel Road along Newton B. Drury Scenic Parkway, 41°24′18″N, 124°1′48″W, 40 m above ground, 2002, *Williams* 198 (HSC); 430 m north-east of Cal Barrel Road's intersection with Newton B. Drury Scenic Parkway, 41°22′15″N, 124°0′48″W, 40 m above ground, 2007, *Williams* 1293 (HSC), 45 m above ground, 2007, *Williams* 1300 (HSC), 50 m above ground, 2007, *Williams* 1282 (UPS), 55 m above ground, 2007, *Williams* 1289 (HSC), 80 m above ground, 2007, *Williams* 1298 (HSC); 320 m south, south-east of Cal Barrel Road's intersection with Newton B. Drury Scenic Parkway, 41°22′10″N, 124°0′49″W, 50 m above ground, 2002, *Williams* 210 (UPS); Redwood National Park, flood plain of Redwood Creek, Tall Trees Grove, 41°12′38″N, 124°0′37″W, 60 m above ground, 2007, *Antoine* MB#1 (HSC); Humboldt Redwoods State Park, 110 m south of parking lot at Lower Bull Creek Flats, 40°20′30″N, 123°56′29″W, 25 m above ground, 2007, *Williams* 1278 (HSC), 40 m above ground, 2007, *Williams* 1221 (HSC), 45 m above ground, 2007, *Williams* 1279 (HSC); 270 m west, south-west of the entrance to Women's Federation Grove, 40°20′33″N, 123°56′8″W, 50 m above ground, 2007, *Williams* 891 (HSC), 55 m above ground, 2007, *Williams* 895 (HSC), 65 m above ground, 2002, *Williams* 206 (UPS), 75 m above ground, 2007, *Williams* 901 (HSC); 265 m west, south-west of the entrance to Women's Federation Grove, 40°20′33″N, 123°56′7″W, 60 m above ground, 2007, *Williams* 902 (HSC).

Discussion

Calicium sequoiae is morphologically distinguished from other known *Calicium* species by its stalks that react I+ blue, mature spores that are ornamented with spiral ridges, and apothecia that produce prominent white pruina. It is also the only *Calicium* known to produce thamnolic acid as a major secondary substance. Genetically close relatives include *C. adspersum*, *C. chlorosporum*, *C. lenticulare*, *Cyphelium notarisii*, and *C. tigillare* (Fig 2; see Tibell 2003, 2006 for a discussion of paraphyly in *Calicium*). *Calicium adspersum* bears a strong resemblance to *C. sequoiae*; both species possess stalks reacting I+ blue, spores with spiral ridges, and clavate asci. However, *C. adspersum* has a yellow pruina on the apothecia and produces a grey, verrucose thallus that reacts K+ red, whereas *C. sequoiae* has a white pruina on the apothecia and produces a yellow to green granular thallus that reacts K+ yellow. *Calicium chlorosporum*, which also produces spores ornamented with spiral ridges, has a pale yellow thallus that is similar to some forms of *C. sequoiae*, but it differs by possessing I− stalks, cylindrical asci, and a Pd+ yellow, UV+ yellow thallus, compared to the Pd+ orange, UV− thallus of *C. sequoiae*. Furthermore, *C. chlorosporum* has a tropical to subtropical distribution (Tibell 1994) and is not known from the Pacific Northwest. Morphological similarities between *C. sequoiae* and *C. lenticulare* include I+ blue stalks and white pruina, but in *C. lenticulare* the spores are ornamented with minute warts or areolae, and the spot tests are all negative. Although *Cyphelium notarisii* and *C. tigillare* are also genetically close to *Calicium sequoiae*, their apothecia are immersed within verrucae rather than stalked.

Calicium contains at least 33 species worldwide, with 13 producing spirally ridged spores and five possessing I+ blue stalks. Only *C. adaequatum* Nyl., *C. adspersum*, and *C. sequoiae* share the combination of spirally ridged spores and I+ blue stalks; thus these characters are very useful for identifying *C. sequoiae*. *Calicium adaequatum* has a very thin, verrucose-areolate thallus, cylindrical asci, and negative spot tests, whereas *C. sequoiae* has a granular thallus, clavate asci, and reacts K+ yellow, Pd+ orange. Apart from *C. lenticulare*, the only additional *Calicium* that possesses I+ blue stalks is *C. muriformis* Tibell, but that species produces submuriform spores and is known only from Japan (Tibell & Thor 2003).

The addition of *C. sequoiae* did not substantially alter the phylogeny of Tibell (2006); four major clades remained well-supported, and species did not move between clades (Fig. 2). Clade I retained its original configuration. Clade II housed *C. sequoiae*, but relationships among the species were still poorly resolved. *Cyphelium notarisii* and *C. tigillare* were sister to each other with

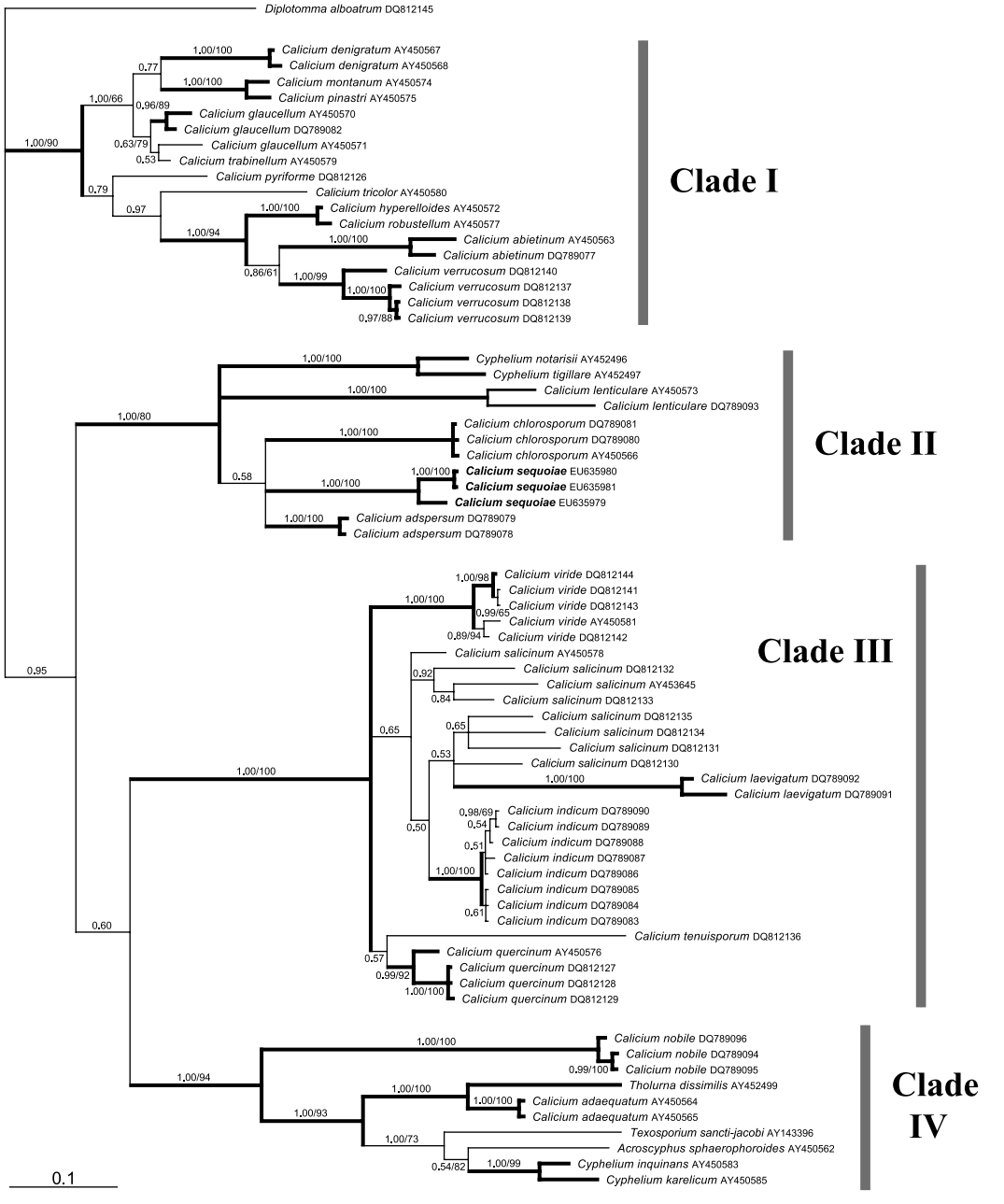

FIG. 2. ITS rDNA phylogeny featuring 30 species of calicioid lichens in the *Physciaceae* plus *Diplotomma alboatrum* as an outgroup. Majority-rule consensus tree of 9000 trees sampled from a 1 000 000 generation MCMC Bayesian tree sampling under the GTR+G+I model. The first value at branches indicates posterior probability. The second value indicates bootstrap support obtained in a MP analysis of the same alignment (heuristic search, TBR branch swapping, 1000 replicates). Thick branches are strongly supported with posterior probability and bootstrap values at least 0·95 and 80, respectively. Scale bar indicates number of substitutions per site. GenBank accession numbers follow the names of the taxa. The recognition of four major clades is based on Tibell (2006).

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high support. *Calicium adspersum*, *C. chlorosporum* and *C. lenticulare* were distinctive in the sequence comparisons and also morphologically well-characterized. We could not, however, find any morphological synapomorphies uniting Clade II. Among these species in Clade II we found zero uniting morphological synapomorphies. Stalks differ from nonexistent to thin and wiry, ascus shape ranges from narrowly cylindrical to broadly clavate, and spore ornamentation varies from smooth to minute warts or spiral ridges. Moreover, members of this clade produce a high diversity of secondary metabolites, including β-orcinol depsides, β-orcinol depsidones, dibenzofurans, pulvinic acid derivatives, and xanthones, representing very different biosynthetic pathways. Despite these seemingly recalcitrant morphological and chemical characters, the clustering of species into this clade received high support. Clade III preserved the original configurations in its well-supported branches and the circumscription of *C. salicinum* remain unresolved. Clade IV did not change.

The distribution and ecology of *C. sequoiae* suggest that it may be a redwood forest endemic with narrow habitat requirements, but other environments should be explored for this species. Temperate forests dominated by large, old members of *Cupressaceae* that share similar bark textural characteristics to redwood provide a possible habitat. In coastal Pacific Northwest, *Chamaecyparis lawsoniana* (A. Murray) Parlatore (Port Orford-cedar), *Thuja plicata* Donn ex D. Don (western redcedar), and *Xanthocyparis nootkatensis* (D. Don) Farjon & D. K. Harder (yellow-cedar) should be examined. Its presence on giant sequoia, the genetically and geographically closest relative to redwood (Farjon 2005), would imply a relictual distribution similar to *Mycocalicium sequoiae* (Rikkinen 2003*c*). Finally, South American coastal temperate forests containing *Fitzroya cupressoides* (Molina) Johnston (alerce) could reveal an antitropical distribution similar to other *Calicium* documented from that region (Tibell 1994, 1998).

Key to the species of *Calicium* from the Pacific Northwest

Calicium diversity in the Pacific Northwest of North America bears a striking resemblance to that of the Nordic countries, including Denmark, Finland, Norway, and Sweden. Thus, detailed descriptions and colour images for all species included in this key (except *C. sequoiae*) can be found in Tibell (1999*b*). Ascospore ornamentation is discernable at a magnification of × 1000. Identification of some species depends upon the stalks reacting I+ blue, which is best seen by mounting whole apothecia in K and then wicking I beneath the coverslip.

1 Substratum rock 2
Substratum bark or wood 3

2 (1) Apothecia short (0·5–0·6 mm) and stout (<7 times longer than stalk width); thallus granular to leprose, thick; on overhanging siliceous rock . . . . . ***C. corynellum* (Ach.) Ach.**
Apothecia long (>1·0 mm) and slender (>7 times longer than stalk width); thallus granular to verrucose; typically epiphytic . . . . . ***C. viride* Pers.**

3 (1) Capitulum pruinose, especially on excipulum rim and lower surface 4
Capitulum lacking pruina 13

4 (3) Pruina yellow to brown 5
Pruina white to greyish white 8

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5 (4) Asci clavate, spore arrangement bi-to triseriate 6
Asci cylindrical, spore arrangement uniseriate 7

6 (5) Pruina yellow; thallus grey, K+ red, Pd+ yellow to orange; stalk I+ blue (sometimes weak) . . . . . ***C. adspersum* Pers.**
Pruina brown; thallus intense green, all spot tests negative . . ***C. viride* Pers.**

7 (5) Pruina rusty brown; thallus K+ dull yellow, KC+ dull yellow turning orange, Pd+ pale yellow or Pd − . . . . . ***C. salicinum* Pers.**
Pruina yellow; all spot tests negative . . . . . ***C. trabinellum* (Ach.) Ach.**

8 (4) Stalk I+ blue 9
Stalk I − 10

9 (8) Mature spores ornamented with spiral ridges and/or irregular cracks; thallus K+ yellow, Pd+ orange . . . . . ***C. sequoiae* Williams & Tibell**
Mature spores ornamented with minute warts or areolae; all spot tests negative . . . . . ***C. lenticulare* Ach.**

10 (8) Asci clavate, spore arrangement bi-to triseriate 11
Asci cylindrical, spore arrangement uniseriate to rarely biseriate 12

11 (10) Mature spores ornamented with faint irregular cracks; thallus grey to greenish grey, Pd+ weakly yellow, UV+ blue; pruina faint . . . . . ***C. parvum* Tibell**
Mature spores ornamented with spiral ridges and/or irregular cracks; thallus yellow to yellowish green, Pd+ orange, UV − ; pruina prominent . . . . . ***C. sequoiae* Williams & Tibell**

12 (10) Mature spores ornamented with spiral ridges and/or irregular cracks; thallus episubstratic, dull grey, K+ yellow to red, Pd+ yellow; pruina prominent . . . . . ***C. quercinum* Pers.**
Mature spores ornamented with longitudinally oriented ridges fragmented by cracks; thallus endosubstratic or episubstratic and dark greyish green, all spot tests negative; pruina faint . . . . . ***C. glaucellum* Ach.**

13 (3) Stalk I+ blue 14
Stalk I − 15

14 (13) Mature spores ornamented with minute warts or areolae . ***C. lenticulare* Ach.**
Mature spores ornamented with spiral ridges . . . . . ***C. adaequatum* Nyl.**

15 (13) Asci clavate, spore arrangement bi- to triseriate 16
Asci cylindrical, spore arrangement uniseriate 17

16 (15) Mature spores ornamented with faint irregular cracks; thallus K+ dull yellow, Pd+ weakly yellow, UV+ blue . . . . . ***C. parvum* Tibell**
Mature spores ornamented with spiral ridges and/or substantial irregular cracks; all spot tests negative . . . . . ***C. viride* Pers.**

17 (15) Mature spores 11·5–15·0 μm long, ornamented with minute warts, areolae, or with some irregular cracks when old; asci 45–60 μm long . . ***C. abietinum* Pers.**
Mature spores 9·0–13·0 μm long, ornamented with longitudinally oriented ridges fragmented by irregular cracks; asci 35–42 μm long . . . ***C. glaucellum* Ach.**

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