



Revisiting the phylogeny of Ocellularieae, the second largest tribe within Graphidaceae (lichenized Ascomycota: Ostropales)

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Abstract

We present an updated 3-locus molecular phylogeny of tribe Ocellularieae, the second largest tribe within subfamily Graphidoideae in the Graphidaceae. Adding 165 newly generated sequences from the mitochondrial small subunit rDNA (mtSSU), the nuclear large subunit rDNA (nuLSU), and the second largest subunit of the DNA-directed RNA polymerase II (*RPB2*), we currently distinguish 218 species among the sequenced material, including the outgroup. This corresponds to almost half the species at this point recognized within this tribe. The newly generated sequences include 23 newly described species and one newly described genus published elsewhere in this volume. For the first time, *Sarcographina cyclospora* Müll. Arg., in spite of its distinctly lirellate ascomata, is shown to belong in tribe Ocellularieae, as strongly supported sister to *Ocellularia inturgescens* (Müll. Arg.) Mangold. The following six new combinations are proposed: *Melanotrema lynceodes* (Nyl.) Rivas Plata, Lücking & Lumbsch, *Ocellularia curranii* (Vain.) Kraichak, Lücking & Lumbsch, *O. khasiana* (Patw. & Nagarkar) Kraichak, Lücking & Lumbsch, *O. cinerea* (Müll. Arg.) Kraichak, Lücking & Lumbsch, *O. erodens* (R. C. Harris) Kraichak, Lücking & Lumbsch, and *O. laeviuscula* (Nyl) Kraichak, Lücking & Lumbsch. Further, the new name *Ocellularia hernandeziana* Kraichak, Lücking & Lumbsch is introduced for *Myriotrema ecorticatum*. The nomenclatural status of the name *Ocellularia microstoma* is clarified.

Key words: *Ampliotrema*, *Glaucotrema*, phylogenetic resolution, *Redingeria*, *Reimnitzia*, *Rhabdodiscus*, *Sarcographina*, *Stegobolus*, supermatrix

Introduction

The two largest families of lichenized ascomycetes are the crustose Graphidaceae and the predominantly foliose and fruticose Parmeliaceae. With a recent increase in species discovery, mainly in tropical regions, Graphidaceae

has surpassed Parmeliaceae in terms of global species richness, with over 2,500 species currently known and approximately 4,300 species predicted (Lücking *et al.* 2014). Graphidaceae contains four subfamilies, Fissurinoideae, Gomphilloideae, Graphidoideae, and Redonographoideae (Rivas Plata *et al.* 2012a; Lücking *et al.* 2013), among which Graphidoideae contains probably more than 75% of the species. Within that subfamily, three large tribes are currently recognized, besides several smaller clades: Graphideae, Ocellularieae, and Thelotremateae (Rivas Plata *et al.* 2012a, b).

Graphideae, containing the large genus *Graphis* Adanson (1763: 11) and otherwise the bulk of species formerly classified in Graphidaceae s.str., is the largest tribe, but recent new species discoveries, especially in the megadiverse genus *Ocellularia* Meyer (1825: 327) s.lat., have increased the known species richness in tribe Ocellularieae to the point that it now approaches the size of Graphideae. This is probably due to the fact that Ocellularieae predominantly contains species confined to undisturbed rain forests (Hale 1974, 1978, 1981; Rivas Plata *et al.* 2008), whereas Graphideae and Thelotremateae are more frequently found in semi-exposed situations in montane forests, making them more readily available for collection and decreasing the possibility for additional new species to be discovered. Hence, increased efforts to sample the diversity of Graphidaceae in undisturbed, often remote rain forest areas will mostly result in novel taxa in the genus *Ocellularia* s.lat. and its relatives. This is also shown by the contribution in this volume, where 67 of the 170 newly described species correspond to tribe Ocellularieae and only 41 to tribe Graphideae.

Tribe Ocellularieae as circumscribed by Rivas Plata *et al.* (2012b), when excluding the *Leptotrema* Mont. & Bosch in Miquel (1855: 483) clade (Lücking *et al.* 2013) principally corresponds to the genera *Myriotrema* Fée (1825: 34) s.lat. and *Ocellularia* s.lat. as circumscribed by Hale (1980). A few species previously ascribed to these genera are now included in *Clandestinotrema* Rivas Plata *et al.* (2012a: 116), *Cruentotrema* Rivas Plata *et al.* (2012a: 119), and *Pycnotrema* Rivas Plata *et al.* (2012a: 120), classified in subfamily Fissurinoideae (Rivas Plata *et al.* 2012a). The very wide traditional generic concept (*Myriotrema* and *Ocellularia*) for taxa now placed within tribe Ocellularieae (Hale 1980) was first challenged by Frisch *et al.* (2006), who reinstated or newly described the genera *Ampliotrema* Kalb ex Kalb in Frisch *et al.* (2006: 81), *Fibrillithecis* Frisch in Frisch *et al.* (2006: 135), *Gyrotrema* Frisch in Frisch *et al.* (2006: 379), *Melanotrema* Frisch in Frisch *et al.* (2006: 382), *Redingeria* Frisch in Frisch *et al.* (2006: 402), and *Stegobolus* Montagne (1845: 4), for morphologically and, in part, genetically distinct segregates of *Myriotrema* s.lat. and *Ocellularia* s.lat. This concept was further expanded based on a broad phylogeny of this group, introducing the additional genera *Compositrema* Rivas Plata *et al.* (2012b: 1172), *Glaucotrema* Rivas Plata & Lumbsch in Rivas Plata *et al.* (2012b: 1174), and *Rhabdodiscus* Vainio (1921: 184) (Rivas Plata *et al.* 2012b). It was also recognized that tribe Ocellularieae contains further, unnamed genus-level lineages, whereas the two genera *Ampliotrema* and *Gyrotrema* do not form monophyletic groups that are distinct from *Ocellularia* s.str (Rivas Plata *et al.* 2012b).

In this contribution, we present an updated molecular phylogeny of tribe Ocellularieae, including an additional 131 OTUs and distinguishing 80 further species compared to our previous study (Rivas Plata *et al.* 2012b). We discuss the individual clades in detail and highlight the phylogenetic position of 23 new taxa described elsewhere in this volume (Aptroot 2014; Lücking 2014; Sipman 2014; Kalb & Jia 2014; Lendemmer & Harris 2014; Cáceres *et al.* 2014; Ferraro *et al.* 2014; Mangold *et al.* 2014; Mercado-Díaz *et al.* 2014; Paping *et al.* 2014a, b; Peláez *et al.* 2014; Poengsungnoen *et al.* 2014a, b; Rivas Plata *et al.* 2014; Sutjaritturakan *et al.* 2014; Van den Broeck *et al.* 2014; Weerakoon *et al.* 2014).

Material and Methods

A total of 165 new sequences of the mtSSU rDNA (94), nuLSU rDNA (56) and the *RPB2* gene (15) were obtained from 131 ingroup OTUs representing 75 species in tribe Ocellularieae. In addition, 432 sequences were used from our previous analyses, including the same outgroup, representing an additional 143 species after taxonomic revision, five more than distinguished previously (Rivas Plata *et al.* 2012b, 2013; Table 1).

New sequences were generated for this study using the Sigma REExtract-N-Amp Plant PCR Kit (St. Louis, Missouri, USA) for DNA isolation following the manufacturer's instructions, except that 40 µL of extraction buffer and 40 µL dilution buffer were used. DNA dilutions (10x) were used in PCR reactions of the genes coding for the nuLSU, mtSSU and *RPB2*. Primers for amplification were: (a) for nuLSU: AL2R (Mangold *et al.* 2008a), and nu-

LSU-1125-3' (= LR6) (Vilgalys & Hester 1990), (b) for mtSSU: mr-SSU1 and Mr-SSU3R (Zoller *et al.* 1999), and (c) for *RPB2*: fRPB2-7cF and fRPB2-11aR (Liu *et al.* 1999). PCR reactions contained 4.5 µL R4775 Sigma REDExtract-N-Amp™ PCR ReadyMix, 0.5 µL of each primer (10 µM), 2 µL genomic DNA extract and 2 µL distilled water for a total of 10 µL. Thermal cycling parameters were: (1) for nuLSU: initial denaturation for 5 min at 94°C, followed by 35 cycles of 30 s at 95°C, 30 s at 58°C, 1 min at 72°C, and a final elongation for 10 min at 72°C; (2) for mtSSU: initial denaturation for 5 min at 95°C, followed by 35 cycles of 45 s at 94°C, 1 min at 50°C, 1 min 30 s at 72°C, and a final elongation for 10 min at 72°C; and (3) for *RPB2*: initial denaturation for 3 min at 95°C, then 1 min at 95°C, and 37 cycles of 1 min at 57°C, 1 min at 58°C, 1 min at 59°C, 1 min at 60°C, 1 min at 61°C, 1 min at 62°C, 1 min at 63°C, 1 min at 64°C and 1.5 min at 72°C, and a final elongation for 10 min at 72°C. Samples were visualized on a 1% ethidium bromide-stained agarose gel under UV light and bands were gel extracted, heated at 70° C for 10 minutes, cooled to 45° C for 5 minutes, treated with 1 µL GELase (Epicentre Biotechnologies, Madison, WI, USA) and incubated at 45° C for at least 24 hours. The 10–µl cycle sequencing reactions consisted of 1–1.5 µl of Big Dye version 3.1 (Applied Biosystems, Foster City, California, U.S.A.), 2.5–3 µl of Big Dye buffer, 6 µM primer, 0.75–2 µl gelased PCR product and water. Samples were sequenced with PCR primers. The cycle sequencing conditions were as follows: 96° C for 1 minute, followed by 25 cycles of 96° C for 10 seconds, 50° C for 5 seconds and 60° C for 4 minutes. Samples were precipitated and sequenced using Applied Biosystems 3730 DNA Analyzer (Foster City, California, U.S.A.), sequences were assembled in SeqMan 4.03 (DNASTAR) and submitted to GenBank (Table 1).

TABLE 1. Genbank numbers and voucher information of specimens used in this study. For author names see *Index Fungorum* (<http://www.indexfungorum.org>).

Species	Country	Collector	Number	mtSSU	nuLSU	RPB2
<i>Ampliotrema amplius</i>	Brazil	Cáceres	6032	JX420961	[—]	[—]
<i>Ampliotrema amplius</i>	Brazil	Cáceres	6038	JX420962	[—]	[—]
<i>Ampliotrema amplius</i>	Peru	Rivas Plata	FM89	JF828958	JF828973	[—]
<i>Ampliotrema lepadinoides</i>	Peru	Rivas Plata	8extra	[—]	JX421433	[—]
<i>Ampliotrema megalostoma</i>	Brazil	Cáceres	sn	JX420964	[—]	[—]
<i>Ampliotrema megalostoma</i>	Brazil	Cáceres	sn	JX420965	[—]	[—]
<i>Ampliotrema megalostoma</i>	Brazil	Cáceres	sn	JX420966	[—]	[—]
<i>Ampliotrema rimosum</i>	Puerto Rico	Mercado	81	KJ435164	[—]	[—]
<i>Ampliotrema sp. nov.</i>	Venezuela	Lücking	32187	JX420963	JX421432	JX420900
<i>Compositrema borinquense</i>	Puerto Rico	Mercado	F7	KJ435180	[—]	[—]
<i>Compositrema cerebriforme</i>	Venezuela	Lücking	32204	JX421017	JX421471	JX420901
<i>Compositrema isidiofarinosum</i>	Venezuela	Kalb	sn	JX421018	JX421472	JX420909
<i>Compositrema isidiofarinosum</i>	Puerto Rico	Mercado	257	KJ435175	[—]	[—]
<i>Compositrema thailandicum</i>	Thailand	Lumbsch	19756o	JX421019	JX421473	[—]
<i>Fibrillithecis argentea</i>	Reunion	Kalb	26027	DQ384901	[—]	[—]
<i>Fibrillithecis confusa</i>	Tanzania	Frisch	99Tz748	DQ384902	[—]	[—]
<i>Fibrillithecis platyspora</i>	New Caledonia	Papong	8037	KJ435199	[—]	[—]
<i>Fibrillithecis gibbosa</i>	Australia	Mangold	36vI	[—]	JX421485	[—]
<i>Fibrillithecis gibbosa</i>	Australia	Mangold	31g	EU075573	EU075621	[—]
<i>Fibrillithecis thailandica</i>	Thailand	Lumbsch	19751a	[—]	JX421486	[—]
<i>Glaucotrema emergens</i>	Philippines	Rivas Plata	1099	JX421061	JX421501	JX420862
<i>Glaucotrema glaucophaenum</i>	Venezuela	Kalb	sn	[—]	[—]	JX420902
<i>Glaucotrema glaucophaenum</i>	Thailand	Lumbsch	19751g	[—]	JX421502	[—]
<i>Glaucotrema glaucophaenum</i>	Australia	Lumbsch	19127eA	JX421060	[—]	[—]

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TABLE 1. (Continued)

Species	Country	Collector	Number	mtSSU	nuLSU	RPB2
<i>Glaucotrema</i> sp. nov.	Thailand	Papong	8560	[—]	KJ435152	[—]
<i>Glaucotrema stegoboloides</i>	Brazil	Cáceres	11817	KJ435228	[—]	[—]
<i>Glaucotrema subcostaricense</i>	Tanzania	Frisch	99Tz866	DQ384899	[—]	[—]
<i>Gyrotrema album</i>	Brazil	Cáceres	11349	KJ435209	[—]	[—]
<i>Gyrotrema flavum</i>	Brazil	Cáceres	11417	KJ435212	[—]	[—]
<i>Gyrotrema wirthii</i>	Costa Rica	Lücking	16301	HQ639591	[—]	[—]
<i>Gyrotrema wirthii</i>	Costa Rica	Lücking	16252	JX421071	[—]	[—]
<i>Leptotrema</i> aff. <i>wightii</i>	El Salvador	Lücking	28095	[—]	JF828977	JF828948
<i>Leptotrema wightii</i>	Costa Rica	Nelsen	2034A	EU075574	[—]	[—]
<i>Leptotrema wightii</i>	Costa Rica	Nelsen	2034A	JX421074	EU075622	[—]
<i>Leptotrema wightii</i>	Costa Rica	WillWolf	10043a	[—]	AY605079	[—]
<i>Melanotrema columellatum</i>	Australia	Kalb	34014	DQ384894	[—]	[—]
<i>Melanotrema columellatum</i>	Australia	Kalb	34013	DQ384895	[—]	[—]
<i>Melanotrema lynceodes</i>	Venezuela	Lücking	32020	[—]	[—]	JX420915
<i>Melanotrema lynceodes</i>	Venezuela	Lücking	32021	JX421088	JX421520	JX420907
<i>Melanotrema lynceodes</i>	Australia	Mangold	351	JX421087	[—]	[—]
<i>Melanotrema meiospermoides</i>	Australia	Kalb	34015	DQ384893	[—]	[—]
<i>Melanotrema meiospermum</i>	Tanzania	Frisch	99Tz470a	DQ384890	[—]	[—]
<i>Melanotrema meiospermum</i>	Tanzania	Frisch	99Tz470b	DQ384891	[—]	[—]
<i>Melanotrema platystomum</i>	Brazil	Lücking	31085	DQ384892	[—]	JX420887
<i>Myriochapsa psoromica</i>	Brazil	Cáceres	11606	KJ435211	[—]	[—]
<i>Myriochapsa psoromica</i>	Brazil	Cáceres	sn	JX421009	JX421461	JX420884
<i>Myriotrema</i> aff. <i>hartii</i>	Ecuador	Lücking	26259	JX421089	[—]	[—]
<i>Myriotrema</i> aff. <i>microporum</i>	Australia	Lumbsch	19174a	[—]	JX421521	[—]
<i>Myriotrema</i> aff. <i>myriotremoides</i>	Thailand	Kalb	39044	[—]	KJ435110	KJ435258
<i>Myriotrema album</i>	Philippines	Rivas Plata	1158	JX421090	[—]	[—]
<i>Myriotrema clandestinum</i>	Australia	Lumbsch	19132vA	JF828963	[—]	[—]
<i>Myriotrema ecorticutum</i>	Venezuela	Lücking	32113	JX421091	JX421522	JX420914
<i>Myriotrema erodens</i>	USA	Lücking	26540	[—]	JX421523	[—]
<i>Myriotrema erodens</i>	USA	Lücking	26541a	[—]	JX421524	[—]
<i>Myriotrema erodens</i>	USA	Lücking	26541b	[—]	JX421525	[—]
<i>Myriotrema erodens</i>	Venezuela	Lücking	32039	JX421092	JX421526	JX420897
<i>Myriotrema laeviusculum</i>	Venezuela	Lücking	32057	JX421093	JX421527	JX420893
<i>Myriotrema laeviusculum</i>	Venezuela	Lücking	32100	JX421094	JX421528	JX420920
<i>Myriotrema laeviusculum</i>	Costa Rica	Sipman	47896	[—]	AY605070	[—]
<i>Myriotrema microporum</i>	Australia	Lumbsch	19092o	EU075578	EU075626	[—]
<i>Myriotrema myrioporoides</i>	Venezuela	Lücking	32205	[—]	JX421529	JX420895
<i>Myriotrema neofrondosum</i>	Puerto Rico	Mercado	163	KJ435166	[—]	[—]
<i>Myriotrema neofrondosum</i>	Peru	Rivas Plata	809canopy	JX421099	[—]	JX420880
<i>Myriotrema olivaceum</i>	Cameroon	Frisch	99Ka1533	DQ384900	[—]	[—]
<i>Myriotrema olivaceum</i>	Thailand	Kalb	39107	KJ435181	KJ435111	[—]
<i>Myriotrema olivaceum</i>	Fiji	Lumbsch	20520a	[—]	JX421531	[—]
<i>Myriotrema olivaceum</i>	Australia	Lumbsch	19113f	EU075579	EU075627	[—]
<i>Myriotrema olivaceum</i>	Australia	Lumbsch	19092g	JX421095	EU126645	[—]

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TABLE 1. (Continued)

Species	Country	Collector	Number	mtSSU	nuLSU	RPB2
<i>Myriotrema olivaceum</i>	Australia	Lumbsch	19116d	JX421096	[—]	[—]
<i>Myriotrema olivaceum</i>	Fiji	Lumbsch	20501c	JX421097	[—]	[—]
<i>Myriotrema olivaceum</i>	Australia	Mangold	33v	[—]	JX421530	[—]
<i>Myriotrema olivaceum</i>	Philippines	Rivas Plata	1063A	JX421098	[—]	[—]
<i>Myriotrema subconforme</i>	Australia	Lumbsch	19160p	JX421100	[—]	[—]
<i>Myriotrema subconforme</i>	Philippines	Rivas Plata	1166A	JX421101	[—]	[—]
<i>Nitidochapsa leprieurii</i>	Thailand	Kalb	38882	JX420991	JX421451	JX420930
<i>Nitidochapsa leprieurii</i>	Australia	Mangold	38l	[—]	JX421450	[—]
<i>Ocellularia</i> aff. <i>albobincta</i>	Peru	Rivas Plata	801D	JX421113	JX421543	JX420873
<i>Ocellularia</i> aff. <i>allosporoides</i>	Thailand	Kalb	38813	JX421118	JX421544	JX420925
<i>Ocellularia</i> aff. <i>allosporoides</i>	Thailand	Lumbsch	19756c	[—]	JX421535	[—]
<i>Ocellularia</i> aff. <i>allosporoides</i>	Thailand	Lumbsch	19756e	[—]	JX421536	[—]
<i>Ocellularia</i> aff. <i>ascidioidea</i>	Thailand	Papong	8478	KJ435248	KJ435153	[—]
<i>Ocellularia</i> aff. <i>ascidioidea</i>	Thailand	Papong	8479	KJ435246	[—]	[—]
<i>Ocellularia</i> aff. <i>ascidioidea</i>	Thailand	Papong	8483	KJ435241	[—]	[—]
<i>Ocellularia</i> aff. <i>ascidioidea</i>	Thailand	Papong	8496	KJ435232	KJ435143	[—]
<i>Ocellularia</i> aff. <i>baileyi</i>	Australia	Lumbsch	19105a	JX421127	[—]	[—]
<i>Ocellularia</i> aff. <i>baileyi</i>	Australia	Lumbsch	19110p	JX421128	[—]	[—]
<i>Ocellularia</i> aff. <i>baileyi</i>	Australia	Mangold	29aa	JX421129	[—]	[—]
<i>Ocellularia</i> aff. <i>baileyi</i>	Australia	Mangold	39m	JX421130	[—]	[—]
<i>Ocellularia</i> aff. <i>baileyi</i>	New Caledonia	Papong	7982	KJ435188	KJ435115	KJ435264
<i>Ocellularia</i> aff. <i>cavata</i>	Australia	Mangold	34zc	JX421103	[—]	[—]
<i>Ocellularia</i> aff. <i>cavata</i>	New Caledonia	Papong	8257	KJ435205	KJ435129	[—]
<i>Ocellularia</i> aff. <i>crocea</i>	Puerto Rico	Mercado	218	KJ435168	[—]	[—]
<i>Ocellularia</i> aff. <i>crocea</i>	Puerto Rico	Mercado	F16	KJ435169	KJ435107	KJ435253
<i>Ocellularia</i> aff. <i>diacida</i>	Australia	Mangold	34i	[—]	JX421553	[—]
<i>Ocellularia</i> aff. <i>diminuta</i>	Peru	Rivas Plata	801A	JX421157	JX421563	JX420872
<i>Ocellularia</i> aff. <i>diminuta</i>	Peru	Rivas Plata	807B	JX421158	[—]	[—]
<i>Ocellularia</i> aff. <i>dolichotata</i>	India	Lumbsch	19730f	[—]	KJ435105	JX420852
<i>Ocellularia</i> aff. <i>dolichotata</i>	Costa Rica	Sipman	46152	[—]	KJ435104	[—]
<i>Ocellularia</i> aff. <i>domingensis</i>	Tanzania	Frisch	99Tz1145	DQ384881	[—]	[—]
<i>Ocellularia</i> aff. <i>domingensis</i>	Australia	Mangold	19j	JX421104	[—]	[—]
<i>Ocellularia</i> aff. <i>fumosa</i>	Thailand	Papong	8576	KJ435231	[—]	[—]
<i>Ocellularia</i> aff. <i>fumosa</i>	Peru	Rivas Plata	809canopy	JX421105	[—]	JX420879
<i>Ocellularia</i> aff. <i>interposita</i>	Thailand	Lumbsch	20203b	JX421165	JX421566	[—]
<i>Ocellularia</i> aff. <i>laeviusculoides</i>	Thailand	Lumbsch	20200j	JX421106	JX421540	[—]
<i>Ocellularia</i> aff. <i>laeviusculoides</i>	Thailand	Lumbsch	20206a	JX421107	JX421541	[—]
<i>Ocellularia</i> aff. <i>minutula</i>	Australia	Lumbsch	19125g	[—]	JX421542	[—]
<i>Ocellularia</i> aff. <i>obturascens</i>	USA	Lücking	26553b	[—]	JX421579	[—]
<i>Ocellularia</i> aff. <i>obturascens</i>	USA	Lücking	26553a	JF828967	JF828979	[—]
<i>Ocellularia</i> aff. <i>obturascens</i>	USA	Lücking	26554	JX421177	[—]	[—]
<i>Ocellularia</i> aff. <i>obturascens</i>	USA	Lücking	26552	JX421178	[—]	[—]
<i>Ocellularia</i> aff. <i>perforata</i>	Australia	Lumbsch	19092t	[—]	AY605073	[—]
<i>Ocellularia</i> aff. <i>perforata</i>	Costa Rica	Sipman	44335	[—]	AY605081	[—]

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TABLE 1. (Continued)

Species	Country	Collector	Number	mtSSU	nuLSU	RPB2
<i>Ocellularia</i> aff. <i>profunda</i>	Australia	Lumbsch	19123k	EU075590	EU075636	[—]
<i>Ocellularia</i> aff. <i>profundadactyls</i>	Australia	Lumbsch	19116j	[—]	JX421586	[—]
<i>Ocellularia</i> aff. <i>profundadactyls</i>	Australia	Lumbsch	19116c	EU075588	EU075635	[—]
<i>Ocellularia</i> aff. <i>pseudochapsa</i>	Brazil	Cáceres	11726	[—]	KJ435135	[—]
<i>Ocellularia</i> aff. <i>pseudochapsa</i>	Brazil	Cáceres	11980	[—]	KJ435133	[—]
<i>Ocellularia</i> aff. <i>vezdana</i>	Panama	Lüicking	27312	JX421111	[—]	[—]
<i>Ocellularia</i> aff. <i>zamboangensis</i>	Thailand	Kalb	39106	KJ435183	KJ435112	[—]
<i>Ocellularia albocincta</i>	Thailand	Kalb	38891	JX421114	[—]	[—]
<i>Ocellularia albocincta</i>	Australia	Mangold	43o	EU075585	EU075633	[—]
<i>Ocellularia albocincta</i>	Australia	Mangold	34a	JX421112	[—]	[—]
<i>Ocellularia albohallina</i>	New Caledonia	Papong	8294	KJ435206	[—]	[—]
<i>Ocellularia albula</i>	Peru	Rivas Plata	1canopy	JX421115	[—]	[—]
<i>Ocellularia allosporoides</i>	Vietnam	Gueidan	3076G	KJ435157	[—]	[—]
<i>Ocellularia allosporoides</i>	Thailand	Lüicking	24110	JX421116	[—]	[—]
<i>Ocellularia allosporoides</i>	Thailand	Lüicking	24130	JX421117	[—]	[—]
<i>Ocellularia allosporoides</i>	Thailand	Lumbsch	20200a	[—]	JX421545	[—]
<i>Ocellularia allosporoides</i>	Thailand	Lumbsch	20204a	JX421119	JX421546	[—]
<i>Ocellularia arecae</i>	Australia	Mangold	32zd	JX421121	JX421547	[—]
<i>Ocellularia ascidioidea</i>	New Caledonia	Papong	7511	KJ435201	KJ435125	KJ435267
<i>Ocellularia ascidioidea</i>	New Caledonia	Papong	7512	KJ435200	KJ435124	KJ435266
<i>Ocellularia auberianoides</i>	USA	Lüicking	26549	JX421122	JX421548	[—]
<i>Ocellularia auberianoides</i>	USA	Lüicking	26548	JX421123	JX421549	[—]
<i>Ocellularia australiana</i>	Australia	Lumbsch	19151u	EU075595	EU075641	[—]
<i>Ocellularia australiana</i>	Australia	Lumbsch	19133g	JX421124	[—]	[—]
<i>Ocellularia australiana</i>	Australia	Lumbsch	19151l	JX421125	[—]	[—]
<i>Ocellularia australiana</i>	Australia	Mangold	25f	JX421126	JX421550	[—]
<i>Ocellularia austropacifica</i>	New Caledonia	Papong	8064	KJ435189	KJ435116	KJ435265
<i>Ocellularia austropacifica</i>	New Caledonia	Papong	8066	KJ435187	KJ435114	KJ435263
<i>Ocellularia austropacifica</i>	New Caledonia	Papong	8074	KJ435190	KJ435117	[—]
<i>Ocellularia bahiana</i>	Costa Rica	Nelsen	2032a	[—]	AY605067	[—]
<i>Ocellularia barroensis</i>	Brazil	Cáceres	11269	KJ435221	[—]	[—]
<i>Ocellularia bonplandii</i>	Australia	Lumbsch	19127z	JX421131	EU126646	[—]
<i>Ocellularia carassensis</i>	Panama	Lüicking	27015a	JX421132	[—]	[—]
<i>Ocellularia cavata</i>	Cameroon	Frisch	99Ka392	DQ384878	[—]	[—]
<i>Ocellularia cavata</i>	Cameroon	Frisch	99Ka403	DQ384879	DQ431935	[—]
<i>Ocellularia chiriquiensis</i>	Brazil	Lüicking	30232	JX421133	[—]	[—]
<i>Ocellularia chiriquiensis</i>	Brazil	Lüicking	30221a	JX421134	[—]	[—]
<i>Ocellularia chiriquiensis</i>	Brazil	Lüicking	30242	JX421135	[—]	[—]
<i>Ocellularia chiriquiensis</i>	Brazil	Lüicking	30232	JX421136	[—]	[—]
<i>Ocellularia chiriquiensis</i>	Venezuela	Lüicking	26098	JX421137	[—]	[—]
<i>Ocellularia chiriquiensis</i>	Australia	Mangold	18d	EU075582	EU075629	[—]
<i>Ocellularia chonestoma</i>	New Caledonia	Papong	7988	KJ435208	[—]	[—]
<i>Ocellularia cicra</i>	Peru	Rivas Plata	108Db	[—]	JX421552	[—]
<i>Ocellularia cicra</i>	Peru	Rivas Plata	8extra	JX421138	[—]	JX420869

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TABLE 1. (Continued)

Species	Country	Collector	Number	mtSSU	nuLSU	RPB2
<i>Ocellularia cicra</i>	Peru	Rivas Plata	108Da	JX421139	JX421551	[—]
<i>Ocellularia cinerea</i>	Australia	Lumbsch	19056b	KJ435161	[—]	[—]
<i>Ocellularia confluens</i>	Australia	Lumbsch	19083	JX421141	[—]	[—]
<i>Ocellularia conformalis</i>	Brazil	Cáceres	6004a	JX421142	[—]	[—]
<i>Ocellularia conformalis</i>	Brazil	Cáceres	6004b	JX421143	[—]	[—]
<i>Ocellularia conformalis</i>	Brazil	Cáceres	6033	JX421144	[—]	[—]
<i>Ocellularia conformis</i>	Panama	Lücking	sn	JX421145	[—]	[—]
<i>Ocellularia cryptica</i>	Costa Rica	Lücking	15215	[—]	AY605083	[—]
<i>Ocellularia diacida</i>	Australia	Lumbsch	19120jB	EU075583	EU075630	[—]
<i>Ocellularia diacida</i>	Australia	Lumbsch	19120jD	JF828965	[—]	[—]
<i>Ocellularia diminuta</i>	Brazil	Cáceres	11174	KJ435214	KJ435138	[—]
<i>Ocellularia dolichotata</i>	Thailand	Kalb	38892	JX421146	JX421554	[—]
<i>Ocellularia dolichotata</i>	Thailand	Lumbsch	20202b	[—]	JX421556	[—]
<i>Ocellularia dolichotata</i>	Thailand	Lumbsch	20202b	[—]	JX421557	[—]
<i>Ocellularia dolichotata</i>	Thailand	Lumbsch	20200f	JX421147	[—]	[—]
<i>Ocellularia dolichotata</i>	Thailand	Lumbsch	20200k	JX421148	JX421555	[—]
<i>Ocellularia dolichotata</i>	Thailand	Lumbsch	20202d	JX421149	JX421558	[—]
<i>Ocellularia dolichotata</i>	Thailand	Lumbsch	20203d	JX421150	JX421559	[—]
<i>Ocellularia domingensis</i>	Venezuela	Lücking	32233	JX421151	JX421560	JX420918
<i>Ocellularia endomelaena</i>	Australia	Lumbsch	19136l	JX421152	[—]	[—]
<i>Ocellularia endomelaena</i>	Australia	Mangold	29a	JF828966	[—]	[—]
<i>Ocellularia endomelaena</i>	Australia	Mangold	30zt	JX421153	[—]	[—]
<i>Ocellularia eumorpha</i>	Tanzania	Frisch	99Tz1504	DQ384885	[—]	[—]
<i>Ocellularia eumorpha</i>	Australia	Lumbsch	19151zd	[—]	JX421561	[—]
<i>Ocellularia exigua</i>	Thailand	Papong	8434	KJ435244	[—]	[—]
<i>Ocellularia fecunda</i>	Panama	Lücking	27150	JX421154	[—]	[—]
<i>Ocellularia fecunda</i>	Venezuela	Lücking	32122	JX421155	JX421562	[—]
<i>Ocellularia fenestrata</i>	Peru	Rivas Plata	8extra	JX421156	[—]	[—]
<i>Ocellularia flavostroma</i>	Brazil	Cáceres	11737	[—]	KJ435141	[—]
<i>Ocellularia fumosa</i>	Cameroon	Frisch	99Ka1949	DQ384880	[—]	[—]
<i>Ocellularia fumosa</i>	Thailand	Lumbsch	19756h	[—]	JX421538	[—]
<i>Ocellularia fumosa</i>	Thailand	Lumbsch	19756n	[—]	JX421539	[—]
<i>Ocellularia fuscosporella</i>	New Caledonia	Papong	7757	KJ435192	KJ435119	[—]
<i>Ocellularia gerardii</i>	Peru	Rivas Plata	1canopy	JX421159	JX421564	[—]
<i>Ocellularia halei</i>	Brazil	Cáceres	11071	KJ435218	[—]	[—]
<i>Ocellularia henatomma</i>	Brazil	Cáceres	6013a	JX421160	[—]	[—]
<i>Ocellularia henatomma</i>	Brazil	Cáceres	6013b	JX421161	[—]	[—]
<i>Ocellularia henatommasorediate</i>	Peru	Rivas Plata	809canopy	JX421162	[—]	JX420881
<i>Ocellularia inconspicua</i>	New Caledonia	Papong	8090	KJ435194	KJ435120	[—]
<i>Ocellularia interposita</i>	Thailand	Lumbsch	20202b	JX421163	[—]	[—]
<i>Ocellularia interposita</i>	Thailand	Lumbsch	20201c	JX421164	JX421565	[—]
<i>Ocellularia inturgescens</i>	Australia	Lumbsch	19132w	EU075577	EU075625	[—]
<i>Ocellularia isidiza</i>	Venezuela	Lücking	32059	JX421166	JX421567	JX420923
<i>Ocellularia kalbii</i>	Australia	Lumbsch	19082e	EU075570	EU075618	[—]

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TABLE 1. (Continued)

Species	Country	Collector	Number	mtSSU	nuLSU	RPB2
<i>Ocellularia kalbii</i>	Australia	Lumbsch	19085i	JX421196	[—]	[—]
<i>Ocellularia khasiana</i>	New Caledonia	Papong	7956	[—]	KJ435131	[—]
<i>Ocellularia khasiana</i>	New Caledonia	Papong	8237	[—]	KJ435132	[—]
<i>Ocellularia laeviusculoides</i>	Mexico	Lücking	RLD063b	[—]	JX421568	[—]
<i>Ocellularia laeviusculoides</i>	Mexico	Lücking	RLD063a	EU075586	EU075632	[—]
<i>Ocellularia laeviusculoides</i>	Venezuela	Lücking	32001	JX421167	JX421569	JX420896
<i>Ocellularia laeviusculoides</i>	Venezuela	Lücking	32037	JX421168	JX421570	JX420922
<i>Ocellularia landronii</i>	Brazil	Cáceres	11039	KJ435213	KJ435137	[—]
<i>Ocellularia massalongoi</i>	Cameroon	Frisch	99Ka1799	DQ384882	[—]	[—]
<i>Ocellularia massalongoi</i>	Fiji	Lumbsch	20523j	[—]	JX421571	[—]
<i>Ocellularia massalongoi</i>	Fiji	Lumbsch	20523h	JX421169	[—]	[—]
<i>Ocellularia massalongoi</i>	Australia	Mangold	36m	EU075584	EU075631	[—]
<i>Ocellularia mauritiana</i>	Peru	Rivas Plata	803D	JX421170	[—]	[—]
<i>Ocellularia microsorediata</i>	Peru	Rivas Plata	107Ca	[—]	JX421572	[—]
<i>Ocellularia microsorediata</i>	Peru	Rivas Plata	107Cb	JX421172	JX421573	[—]
<i>Ocellularia microstoma</i>	Australia	Lumbsch	19100q	[—]	JX421574	[—]
<i>Ocellularia microstoma</i>	Australia	Lumbsch	19108c	[—]	EU126648	[—]
<i>Ocellularia microstoma</i>	Japan	Lumbsch	19056b1	[—]	AY605074	[—]
<i>Ocellularia microstoma</i>	Japan	Lumbsch	19056b2	[—]	JX421576	JX420823
<i>Ocellularia microstoma</i>	Australia	Lumbsch	19125r	JX421108	JX421575	[—]
<i>Ocellularia microstoma</i>	Philippines	Rivas Plata	1085B	[—]	JX421577	[—]
<i>Ocellularia microstoma</i>	Philippines	Rivas Plata	1063E	JX421109	[—]	[—]
<i>Ocellularia microstoma</i>	Philippines	Rivas Plata	1193C	JX421110	[—]	[—]
<i>Ocellularia minutula 1</i>	Australia	Lumbsch	19167t	JX421173	JX421578	[—]
<i>Ocellularia minutula 2</i>	Australia	Lumbsch	19155d	KJ435162	[—]	[—]
<i>Ocellularia minutula 2</i>	Australia	Lumbsch	19156g	JX421174	[—]	[—]
<i>Ocellularia mordenii</i>	Puerto Rico	Mercado	238	KJ435170	[—]	[—]
<i>Ocellularia myriotrema</i>	Brazil	Cáceres	11334	KJ435224	[—]	[—]
<i>Ocellularia myriotrema</i>	Brazil	Cáceres	11576	KJ435215	[—]	[—]
<i>Ocellularia natashae</i>	Peru	Rivas Plata	1canopy	JX421175	[—]	JX420877
<i>Ocellularia neocaledonica</i>	New Caledonia	Papong	7551	KJ435207	KJ435130	[—]
<i>Ocellularia neopertusariiiformis</i>	Australia	Mangold	35zf	JX421176	[—]	[—]
<i>Ocellularia oculata</i>	Australia	Kalb	33985	DQ384874	[—]	[—]
<i>Ocellularia oculata</i>	Australia	Kalb	33986	DQ384875	[—]	[—]
<i>Ocellularia oculata</i>	Australia	Lumbsch	19160wA	EU075565	EU075612	[—]
<i>Ocellularia oculata</i>	Fiji	Lumbsch	19817i	JX421377	JX421663	[—]
<i>Ocellularia oculata</i>	Australia	Mangold	33a	EU075564	EU075613	[—]
<i>Ocellularia percolumellata</i>	Brazil	Cáceres	6002a	JX421180	[—]	JX420888
<i>Ocellularia percolumellata</i>	Brazil	Cáceres	6002b	JX421181	[—]	[—]
<i>Ocellularia perforata</i>	Australia	Lumbsch	19120jA	EU075587	EU075634	[—]
<i>Ocellularia perforata</i>	Australia	Lumbsch	19120jC	JX421182	[—]	[—]
<i>Ocellularia perforata</i>	Fiji	Lumbsch	19849	JX421183	[—]	[—]
<i>Ocellularia pertusariiiformis</i>	Philippines	Rivas Plata	1074B	JX421184	[—]	[—]
<i>Ocellularia petrinensis</i>	Venezuela	Lücking	32024	JX421185	JX421532	JX420910

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TABLE 1. (Continued)

Species	Country	Collector	Number	mtSSU	nuLSU	RPB2
<i>Ocellularia philippina</i>	Philippines	Rivas Plata	1070	JX421187	[—]	[—]
<i>Ocellularia philippina</i>	Philippines	Rivas Plata	1135	JX421188	[—]	[—]
<i>Ocellularia plicata</i>	Peru	Rivas Plata	809canopy	JX421189	[—]	[—]
<i>Ocellularia pluriporoides</i>	Brazil	Cáceres	sn	JX421190	JX421580	[—]
<i>Ocellularia polydiscus</i>	Brazil	Cáceres	11021	KJ435217	[—]	[—]
<i>Ocellularia polydiscus</i>	Tanzania	Frisch	99Tz1950	DQ384877	[—]	[—]
<i>Ocellularia polydiscus</i>	Brazil	Lücking	27966	DQ384876	[—]	[—]
<i>Ocellularia portoricensis</i>	Puerto Rico	Mercado	F19	KJ435178	[—]	KJ435256
<i>Ocellularia portoricensis</i>	Puerto Rico	Mercado	F64	KJ435179	[—]	KJ435257
<i>Ocellularia postposita</i>	Tanzania	Frisch	99TZ1879	DQ384873	[—]	[—]
<i>Ocellularia praestans</i>	Panama	Lücking	sn	JX421191	[—]	[—]
<i>Ocellularia praestans</i>	Venezuela	Lücking	32200	JX421192	JX421581	JX420892
<i>Ocellularia praestans</i>	Venezuela	Lücking	32239	JX421193	JX421582	JX420894
<i>Ocellularia praestans</i>	Venezuela	Lücking	32106	JX421194	[—]	JX420899
<i>Ocellularia praestans</i>	Venezuela	Lücking	32236	JX421195	JX421583	JX420911
<i>Ocellularia profunda</i>	Australia	Lumbsch	19077c	[—]	JX421584	[—]
<i>Ocellularia profunda</i>	Australia	Lumbsch	19085h	[—]	EU126647	[—]
<i>Ocellularia profunda</i>	Australia	Lumbsch	19100p	EU075589	AY605082	[—]
<i>Ocellularia profunda</i>	Australia	Lumbsch	19100t	JX421197	[—]	[—]
<i>Ocellularia profunda</i>	Australia	Lumbsch	19100p	JX421198	JX421585	JX420825
<i>Ocellularia pseudochapsa</i>	Brazil	Cáceres	11719	KJ435229	[—]	[—]
<i>Ocellularia pseudochapsa</i>	Brazil	Cáceres	11790	KJ435210	KJ435134	[—]
<i>Ocellularia pseudostromatica</i>	Brazil	Cáceres	11352	KJ435223	KJ435140	[—]
<i>Ocellularia psorbarroensis</i>	Brazil	Cáceres	6007	JX421199	[—]	[—]
<i>Ocellularia psorbarroensis</i>	Peru	Rivas Plata	8extra	JX421200	[—]	[—]
<i>Ocellularia psorbarroensis</i>	Peru	Rivas Plata	108B	JX421201	JX421587	[—]
<i>Ocellularia psorbarroensis</i>	Peru	Rivas Plata	801D	JX421202	JX421588	JX420874
<i>Ocellularia psorbarroensis</i>	Peru	Rivas Plata	801D	JX421203	JX421589	[—]
<i>Ocellularia psorbarroensis</i>	Peru	Rivas Plata	810B	JX421204	JX421590	[—]
<i>Ocellularia psorbarroensis</i>	Peru	Rivas Plata	1canopy	JX421205	JX421591	[—]
<i>Ocellularia psorbarroensis</i>	Peru	Rivas Plata	8extra	JX421206	[—]	[—]
<i>Ocellularia psorbarroensis</i>	Peru	Rivas Plata	1canopy	JX421207	[—]	[—]
<i>Ocellularia pulchella</i>	New Caledonia	Papong	8048	KJ435195	KJ435121	[—]
<i>Ocellularia pyrenuloides</i>	Australia	Kalb	34019	DQ384896	[—]	[—]
<i>Ocellularia pyrenuloides</i>	New Caledonia	Papong	8031	KJ435203	KJ435127	KJ435268
<i>Ocellularia rhabdospora</i>	Puerto Rico	Mercado	F35	KJ435171	[—]	[—]
<i>Ocellularia rhabdospora</i>	Puerto Rico	Mercado	F75	KJ435172	KJ435108	KJ435254
<i>Ocellularia rhabdospora</i>	Puerto Rico	Mercado	F76	KJ435176	[—]	KJ435255
<i>Ocellularia rhicnoporoides</i>	Venezuela	Lücking	32107	JX421209	JX421593	[—]
<i>Ocellularia rhicnoporoides</i>	Thailand	Lumbsch	19750e	JX421208	JX421592	[—]
<i>Ocellularia rhodostroma</i>	Costa Rica	Sipman	44335	[—]	AY605068	[—]
<i>Ocellularia rimosa</i>	Thailand	Kalb	38767	JX421211	[—]	JX420927
<i>Ocellularia rimosa</i>	Australia	Mangold	35b	JX421210	[—]	[—]
<i>Ocellularia rondoniana</i>	Brazil	Cáceres	11335	KJ435216	[—]	[—]

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TABLE 1. (Continued)

Species	Country	Collector	Number	mtSSU	nuLSU	RPB2
<i>Ocellularia rondoniana</i>	Brazil	Cáceres	11852	KJ435222	[—]	[—]
<i>Ocellularia rondoniana</i>	Brazil	Cáceres	11982	KJ435220	KJ435139	[—]
<i>Ocellularia rugosothallina</i>	New Caledonia	Papong	8284	KJ435202	KJ435126	[—]
<i>Ocellularia salmonea</i>	New Caledonia	Papong	7954	KJ435191	KJ435118	[—]
<i>Ocellularia schizidiata</i>	Philippines	Rivas Plata	1106	JX421215	[—]	[—]
<i>Ocellularia soreciate 1</i>	Peru	Rivas Plata	107C	JX421216	[—]	[—]
<i>Ocellularia soreciate 2</i>	Peru	Rivas Plata	808D	JX421217	[—]	[—]
<i>Ocellularia soreciate 3</i>	Puerto Rico	Mercado	247	KJ435177	[—]	[—]
<i>Ocellularia</i> sp. nov. 1	Venezuela	Lücking	32217	JX421120	[—]	JX420921
<i>Ocellularia</i> sp. nov. 3	Thailand	Lücking	24129	JX421179	[—]	[—]
<i>Ocellularia</i> sp. nov. 4	Thailand	Lumbsch	20202e	JX421186	[—]	[—]
<i>Ocellularia</i> sp. nov. 6	Thailand	Papong	8541	KJ435239	KJ435150	[—]
<i>Ocellularia</i> sp. nov. 6	Thailand	Papong	8542	KJ435249	KJ435154	[—]
<i>Ocellularia</i> sp. nov. 6	Thailand	Papong	8552	KJ435236	KJ435147	[—]
<i>Ocellularia</i> sp. nov. 6	Thailand	Papong	8557	KJ435238	KJ435149	[—]
<i>Ocellularia</i> sp. nov. 6	Thailand	Papong	8564	KJ435240	KJ435151	[—]
<i>Ocellularia</i> sp. nov. 6	Thailand	Papong	8566	KJ435233	KJ435144	[—]
<i>Ocellularia</i> sp. nov. 6	Thailand	Papong	8567	KJ435245	[—]	[—]
<i>Ocellularia</i> sp. nov. 6	Thailand	Papong	8568	KJ435237	KJ435148	[—]
<i>Ocellularia</i> sp. nov. 6	Thailand	Papong	8570	KJ435250	KJ435155	[—]
<i>Ocellularia</i> sp. nov. 6	Thailand	Papong	8573	KJ435251	KJ435156	[—]
<i>Ocellularia</i> sp. nov. 7	Thailand	Papong	8574	KJ435252	[—]	[—]
<i>Ocellularia</i> sp. nov. 8	Thailand	Papong	8439	KJ435235	KJ435146	[—]
<i>Ocellularia</i> sp. nov. 8	Thailand	Papong	8458	KJ435247	[—]	[—]
<i>Ocellularia</i> sp.	Vietnam	Gueidan	3086G	KJ435158	[—]	[—]
<i>Ocellularia</i> sp.	Vietnam	Gueidan	3304G	KJ435159	[—]	[—]
<i>Ocellularia</i> sp.	Thailand	Kalb	39042	KJ435185	[—]	KJ435261
<i>Ocellularia</i> sp.	Thailand	Kalb	39092	KJ435182	[—]	KJ435259
<i>Ocellularia</i> sp.	Thailand	Kalb	39091a	KJ435186	[—]	KJ435262
<i>Ocellularia</i> sp.	Thailand	Kalb	38839	JX421214	[—]	JX420931
<i>Ocellularia</i> sp.	Australia	Lumbsch	19161d	[—]	JX421594	[—]
<i>Ocellularia</i> sp.	Australia	Lumbsch	19082a	JX421212	[—]	[—]
<i>Ocellularia</i> sp.	Australia	Mangold	31m	JX421213	[—]	[—]
<i>Ocellularia</i> sp. soreciate 4	Australia	Lumbsch	19144a	[—]	JX421595	[—]
<i>Ocellularia</i> sp. soreciate 4	Australia	Lumbsch	19144d	EU075591	EU075637	[—]
<i>Ocellularia</i> sp. soreciate dactyls	Australia	Mangold	29b	[—]	JX421597	[—]
<i>Ocellularia</i> sp. sterile	Australia	Mangold	32d2	[—]	JX421598	[—]
<i>Ocellularia</i> sp. sterile	Australia	Mangold	35o	[—]	JX421596	[—]
<i>Ocellularia subpraestans</i>	Panama	Lücking	sn	JX421218	[—]	[—]
<i>Ocellularia terebrata</i>	Australia	Lumbsch	19132zd	JF828964	[—]	[—]
<i>Ocellularia terebrata</i>	Australia	Lumbsch	19128mA	JX421219	[—]	[—]
<i>Ocellularia terebrata</i>	New Caledonia	Papong	8256	KJ435198	[—]	[—]
<i>Ocellularia thelotremoides</i>	Tanzania	Frisch	99Tz1122	DQ384884	[—]	[—]
<i>Ocellularia thelotremoides</i>	Venezuela	Lücking	26052	JX421221	[—]	[—]

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TABLE 1. (Continued)

Species	Country	Collector	Number	mtSSU	nuLSU	RPB2
<i>Ocellularia thelotremoides</i>	Australia	Lumbsch	19081j	[—]	EU126649	[—]
<i>Ocellularia thelotremoides</i>	Australia	Lumbsch	19108i	EU075592	EU075638	[—]
<i>Ocellularia thelotremoides</i>	Australia	Lumbsch	19153l	JX421220	[—]	[—]
<i>Ocellularia thelotremoides</i>	Thailand	Papong	8449	KJ435234	KJ435145	[—]
<i>Ocellularia thryptica</i>	Peru	Rivas Plata	103D	JX421222	[—]	[—]
<i>Ocellularia thryptica</i>	Peru	Rivas Plata	8extra	JX421223	[—]	[—]
<i>Ocellularia umbilicata</i>	Puerto Rico	Mercado	242	KJ435173	KJ435109	[—]
<i>Ocellularia urceolaris</i>	Costa Rica	Lücking	21053	JX421224	[—]	[—]
<i>Ocellularia vezdana</i>	Cameroon	Frisch	99Ka1546	DQ384883	[—]	[—]
<i>Ocellularia violacea</i>	Brazil	Cáceres	sn	JX421225	[—]	[—]
<i>Ocellularia violacea</i>	Brazil	Cáceres	sn	JX421226	[—]	[—]
<i>Ocellularia viridipallens</i>	Thailand	Lücking	24131	JX421227	[—]	[—]
<i>Ocellularia vulcanisorediata</i>	Puerto Rico	Mercado	76	KJ435174	[—]	[—]
<i>Ocellularia vulcanisorediata</i>	Puerto Rico	Mercado	4451	KJ435165	KJ435106	[—]
<i>Ocellularia wirthii</i>	Australia	Mangold	25b	JX421228	JX421599	[—]
<i>Ocellularia xanthostromiza</i>	Brazil	Cáceres	11982	KJ435219	[—]	[—]
<i>Ocellularia xanthostromiza</i>	Thailand	Papong	8559	KJ435243	[—]	[—]
<i>Ocellularia xanthostromiza</i>	Peru	Rivas Plata	809canopy	JX421171	[—]	[—]
<i>Redingeria desseiniana</i>	DR Congo	Ertz	14296	KJ145246	KJ145245	[—]
<i>Redingeria glaucoglyphica</i>	Peru	Rivas Plata	802A2	[—]	JX421617	[—]
<i>Redingeria glaucoglyphica</i>	Peru	Rivas Plata	802A1	HQ639601	JX421616	[—]
<i>Redingeria glaucoglyphica</i>	Peru	Rivas Plata	810extra	JX421296	JX421618	[—]
<i>Redingeria microspora</i>	Brazil	Cáceres	6030	JX421297	[—]	[—]
<i>Reimnitzia</i> aff. <i>santensis</i>	India	Lumbsch	19706b	[—]	JX421619	[—]
<i>Reimnitzia santensis</i>	El Salvador	Lücking	28015	HQ639622		JF828952
<i>Reimnitzia santensis</i>	USA	Nelsen	sn	JX443520	[—]	[—]
<i>Reimnitzia santensis</i>	Costa Rica	Will-Wolf	10024b	[—]	JX421620	[—]
<i>Rhabdodiscus</i> aff. <i>asiaticus</i>	New Caledonia	Papong	8020	KJ435193	[—]	[—]
<i>Rhabdodiscus</i> aff. <i>asiaticus</i>	Philippines	Rivas Plata	1054A	JX421298	[—]	[—]
<i>Rhabdodiscus asiaticus</i>	Australia	Kalb	sn	DQ384888	[—]	[—]
<i>Rhabdodiscus auberianus</i>	Brazil	Cáceres	11977	KJ435225	[—]	[—]
<i>Rhabdodiscus crassus</i>	Australia	Lumbsch	19108f	EU075594	EU075640	[—]
<i>Rhabdodiscus emersus</i>	Australia	Kalb	sn	DQ384889	[—]	[—]
<i>Rhabdodiscus integer</i>	Australia	Lumbsch	19108a	JX421299	[—]	[—]
<i>Rhabdodiscus isidiiferus</i>	Venezuela	Lücking	32212	JX421300	JX421621	JX420903
<i>Rhabdodiscus isidiiferus</i>	Venezuela	Lücking	32213	JX421301	JX421622	JX420904
<i>Rhabdodiscus isidiiferus</i>	Venezuela	Lücking	32201	JX421302	JX421623	JX420908
<i>Rhabdodiscus isidiiferus</i>	Venezuela	Lücking	32211	JX421303	JX421624	JX420912
<i>Rhabdodiscus marivelensis</i>	Thailand	Lücking	24115	JX421304	[—]	[—]
<i>Rhabdodiscus neocaledonicus</i>	New Caledonia	Papong	7630	KJ435204	KJ435128	[—]
<i>Rhabdodiscus saxicola</i>	New Caledonia	Papong	8042	KJ435197	KJ435123	[—]
<i>Rhabdodiscus schizostomus</i>	Philippines	Rivas Plata	1165a	JX421305	[—]	[—]
<i>Rhabdodiscus schizostomus</i>	Philippines	Rivas Plata	1165b	JX421306	[—]	[—]
<i>Rhabdodiscus</i> sp.	Vietnam	Gueidan	3039G	KJ435160	[—]	[—]

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TABLE 1. (Continued)

Species	Country	Collector	Number	mtSSU	nuLSU	RPB2
<i>Rhabdodiscus</i> sp.	Fiji	Lumbsch	20501j	JX421307	[—]	[—]
<i>Rhabdodiscus subcavatus</i>	Brazil	Cáceres	6301a	JX421308	[—]	[—]
<i>Rhabdodiscus subcavatus</i>	Brazil	Cáceres	6301b	JX421309	[—]	[—]
<i>Rhabdodiscus subcavatus</i>	Brazil	Cáceres	sn	JX421310	[—]	[—]
<i>Rhabdodiscus subcavatus</i>	Brazil	Cáceres	sn	JX421311	[—]	[—]
<i>Rhabdodiscus subemersus</i>	Tanzania	Frisch	99Tz388D	DQ384886	[—]	[—]
<i>Rhabdodiscus subemersus</i>	Brazil	Lücking	31665	DQ384887	[—]	[—]
<i>Rhabdodiscus thouvenotii</i>	New Caledonia	Papong	8049	KJ435196	KJ435122	[—]
<i>Sarcographina cyclospora</i>	SriLanka	Weerakoon	116A	KJ435230	[—]	[—]
<i>Stegobolus actinotus</i>	Cameroon	Frisch	99Ka1316D	DQ384897	[—]	[—]
<i>Stegobolus</i> aff. <i>berkeleyanus</i>	Australia	Kalb	34020	DQ384898	[—]	[—]
<i>Stegobolus anamorphus</i>	Brazil	Cáceres	11957	[—]	KJ435142	[—]
<i>Stegobolus anamorphus</i>	Brazil	Cáceres	11860	KJ435227	[—]	[—]
<i>Stegobolus anamorphus</i>	Brazil	Cáceres	6003a	JX421329	[—]	[—]
<i>Stegobolus anamorphus</i>	Brazil	Cáceres	6003b	JX421330	[—]	[—]
<i>Stegobolus anamorphus</i>	Peru	Rivas Plata	807D	JX421331	JX421634	[—]
<i>Stegobolus anamorphus</i>	Peru	Rivas Plata	E810D	JX421332	JX421635	[—]
<i>Stegobolus berkeleyanus</i>	Thailand	Lumbsch	20200d	[—]	JX421637	[—]
<i>Stegobolus berkeleyanus</i>	Thailand	Lumbsch	20203e	JX421333	JX421638	[—]
<i>Stegobolus berkeleyanus</i>	Thailand	Papong	8444	KJ435242	[—]	[—]
<i>Stegobolus guianensis</i>	Brazil	Cáceres	11820	KJ435226	[—]	[—]
<i>Stegobolus radians</i>	Venezuela	Lücking	32207	[—]	JX421639	JX420917
<i>Stegobolus subwrightii</i>	Venezuela	Lücking	32202	[—]	JX421636	JX420913
<i>Stegobolus wrightii</i>	Brazil	Cáceres	sn	JX421334	[—]	[—]
<i>Stegobolus wrightii</i>	Brazil	Cáceres	sn	JX421335	[—]	[—]

Sequences were arranged into multiple sequence alignments (MSA) for each gene using BIOEDIT 7.09 (Hall 1999) and automatically aligned with MAFFT using the -auto option (Kato & Toh 2005). The unaligned MSA for the mtSSU and nuLSU gene partitions were also submitted to the GUIDANCE web server at <http://guidance.tau.ac.il> to assess alignment confidence scores for each site (Penn *et al.* 2010a, b). GUIDANCE uses a MAFFT alignment and returns a colored MSA that allows delimiting ambiguously aligned portions of the MSA. These were then excluded from further analysis. Introns were deleted from the nuLSU gene partition because of their random occurrence but kept in the mtSSU partition if consistent within species or species groups. This resulted in alignments of 1000 sites for the mtSSU (334 OTUs), 900 sites for the nuLSU (201 OTUs), and 915 for RPB2 (63 OTUs), for a total of 2815 sites in the combined dataset and 597 out of 1203 possible individual sequences (49.6% cover). After testing for supported topological conflicts (Mason-Gamer & Kellogg 1996; Miadlikowska & Lutzoni 2000; Kauff & Lutzoni 2002), the three genes were combined into a single supermatrix. Individual datasets and the combined supermatrix were subjected to maximum likelihood search using the RAxML-HPC BlackBox 7.3.2 on the Cipres Science Gateway server (Stamatakis 2006; Stamatakis *et al.* 2005, 2008; Miller *et al.* 2010; <http://www.phylo.org/portal2/login!input.action>), with parametric bootstrapping generating 350 replicates as automatically determined by RAxML using a saturation criterion. The universal GTR-Gamma model was chosen for the analysis. For the Bayesian analysis, the data set was partitioned into three parts (one for each locus) and analyzed using MrBAYES 3.1.2 (Huelsenbeck & Ronquist 2001) on the Cipres Science Gateway server. For all loci, the GTR+I+G was chosen as the most optimal substitution model. A run with 10,000,000 generations, starting with a random tree and employing four simultaneous chains, was executed. Heating of chains was set to 0.2. Posterior probabilities were estimated by sampling trees using a variant of Markov Chain Monte Carlo (MCMC) method. Every 1000th tree was sampled to avoid autocorrelation. The first 2,500 trees

were discarded as burn in. A majority-rule consensus tree with average branch lengths was computed from the remaining trees, using the sumt option of MrBAYES. Posterior probabilities were obtained for each clade.

Results and Discussion

The overall topology for tribe Ocellularieae (Fig. 1) mirrors results obtained from earlier studies (Rivas Plata *et al.* 2012b, 2013). The well-supported tribe is divided in three main clades: (1) a large, unsupported clade containing the bulk of the genera except *Ocellularia*, here called the *Myriotrema* clade, (2) a small, strongly supported clade corresponding to the genus *Rhabdodiscus*, and (3) another large, supported clade containing *Nitidochapsa* Parmen *et al.* (2013: 128) and *Ocellularia* s.lat., here called the *Ocellularia* clade. Within the *Myriotrema* clade, the following currently accepted nine genera were recovered as monophyletic with support: *Compositrema*, *Fibrillithecis*, *Glaucotrema*, *Melanotrema*, *Myriochapsa* Parmen *et al.* (2013: 128), *Myriotrema* s.str., *Nitidochapsa*, *Redingeria*, and *Stegobolus*. In addition, the *Myriotrema* clade contains five small clades corresponding to species currently classified as *Myriotrema* or *Ocellularia*: (1) the *M. album* Fée (1825: 104) clade, (2) the *O. pyrenuloides* Zahlbr. in Magnusson & Zahlbruckner (1944: 46) clade, (3) the *O. inturgescens* (Müll. Arg.) Mangold in Mangold *et al.* (2009: 656) clade, (4) the *O. praestans* (Müll. Arg.) Hale (1980: 137) clade, and (5) the *O. profunda* (Stirt.) Mangold *et al.* (2007: 204) clade. The most striking result is the placement of *Sarcographina cyclospora* Müller (1887: 425), a species for a long time misunderstood to represent the muriform-spored counterpart of *Sarcographa* Fée (1825: xxxv, xc, 58; Zahlbruckner 1923; Staiger 2002; Archer 2009), as a lirellate representative of the *Myriotrema* clade, coming out as strongly supported sister to *Ocellularia inturgescens* (Müll. Arg.) Mangold (2009: 656). This placement is in part supported by morphology, since *Sarcographina* features a thallus anatomy composed of large, columnar clusters of calcium oxalate crystals, a feature found in several lineages within tribes Ocellularieae and Leptotremateae but unknown from *Sarcographa* and relatives. Also, the ascospores of *Sarcographina* are reminiscent of those of *Leptotrema*, *Redingeria*, and *Reimnitzia*.

The *Ocellularia* s.lat. clade, containing the bulk of *Ocellularia* species, is not supported, but within this clade, the supported *O. terebrata* (Ach.) Müller (1887: 398) clade is sister to a strongly supported clade that contains the remainder of *Ocellularia* s.lat. *Ocellularia* s.lat. contains several clades of various sizes: the *O. wirthii* Mangold *et al.* (2008b: 364) clade (strongly supported), the *O. baileyi* Müller (1891a: 51) clade (supported), the *O. massalongoi* (Mont.) Hale (1980: 137) clade (strongly supported), the *O. bahiana* (Ach.) Frisch in Frisch *et al.* (2006: 503) clade (strongly supported), the *O. perforata* (Leight.) Müller (1892: 284) clade (strongly supported), sister to *Myriotrema clandestinum* (Fée) Hale (1980: 133), the *O. dolichotata* (Nyl.) Zahlbruckner (1923: 589) clade (strongly supported), the *Ampliotrema* clade [supported but not monophyletic, since the type species, *A. amplius* (Nyl.) Kalb ex Kalb in Frisch *et al.* (2006: 81), falls outside], the *O. eumorpha* (Stirt.) Hale (1980: 136) clade (strongly supported), and *Ocellularia* s.str. (not supported), with the genus *Gyrotrema* nested near its base.

The internal topology of the outgroup (tribe Leptotremateae) suggests that both *Reimnitzia* Kalb (2001: 325) and *Leptotrema* contain an additional, unrecognized species each (Fig. 2). The specimen from India labeled *R. santensis* (Tuck.) Kalb (2001: 325) is phylogenetically distinct from the material from the Neotropics (USA, El Salvador, Costa Rica), from which the type originates. Morphologically, it differs from typical material by the smaller ascomata lacking erect to recurved marginal lobules and by the flask-shaped rather than cylindrical isidia (Fig. 3A–D). Further material from Costa Rica and Sri Lanka (Fig. 3E–F) suggests that the genus *Reimnitzia* might include a number of hitherto unrecognized species, differing chiefly in ascoma morphology. Regarding the genus *Leptotrema*, the specimen of *L. wightii* (Taylor) Müller (1882: 499) from El Salvador does not display morphological differences compared to the material from Costa Rica. Further studies will show whether these specimens warrant status as separate taxa.

In a previous phylogenetic study (Rivas Plata *et al.* 2012b), the sequenced specimens of *Glaucotrema* were considered to represent a single species, *G. glaucophaenum* (Kremp.) Rivas Plata & Lumbsch in Rivas Plata *et al.* (2012b: 1175). In the present analysis, we added two new species, an undescribed species from Thailand and *G. stegoboloides* Cáceres *et al.* (2014) from Brazil, which differs from *G. glaucophaenum* in having larger



FIGURE 1. Best-scoring maximum likelihood tree of tribe Ocellularieae based on a 3-locus dataset, showing major clades. Supported clades are marked with an asterisk. Detailed phylogenies for each portion of the tree, as well as numeric support values, are depicted in Figs 2, 6, 9, 10.



FIGURE 2. Best-scoring maximum likelihood tree of tribe Ocellularieae based on a 3-locus dataset, showing the *Myriotrema* clade. Supported branches are marked by thick lines and both bootstrap support values (70% or higher) and posterior probabilities (0.95 or higher) are given.

ascomata with a complex columella resembling species of the genera *Rhabdodiscus* and *Stegobolus*. The remaining material labeled *G. glaucophaenum* does not form a monophyletic clade (Fig. 2), which suggests that more than one species is involved here. This would not be surprising given that the five specimens originate from five different regions (Venezuela, Tanzania, Thailand, Philippines, Australia) and would be an example that taxa considered pantropical due to morphological similarities actually represent phylogenetically distinct clades. More samples are necessary to clarify this.

The *Ocellularia pyrenuloides* clade contains two well-supported clades (Fig. 2): *O. pyrenuloides* and a second clade including *O. conformalis* (Kremp.) M. Cáceres & Lücking in Cáceres *et al.* (2012: 809) and the newly described *O. vulcanisorediata* Mercado-Díaz *et al.* (2014). Whereas *O. pyrenuloides* is characterized by an unusual stictic acid chemistry, otherwise very rare in this tribe, *O. conformalis* produces psoromic acid and *O. vulcanisorediata* lacks substances. The latter two species have no characters that would separate them from typical species of *Ocellularia*. More sequence data of further species are needed to elucidate the composition of this clade, which either retained general plesiomorphic features within tribe Ocellularieae or evolved *Ocellularia*-like characters in parallel (Rivas Plata & Lumbsch 2011).

Within the strongly supported genus *Melanotrema* (Fig. 2), specimens identified as ***M. lynceodes* (Nyl.) Rivas Plata, Lücking & Lumbsch, comb. nov.** [Mycobank #807660; *Graphis lynceodes* Nyl., *Flora* 69: 174. 1886] from Venezuela and Australia cluster together but without support, suggesting that *Melanotrema lynceodes* as defined here might be polyphyletic. Notably, the type of *Graphis lynceodes* is from tropical Africa, so neither the Venezuelan nor the Australian material might actually represent this species phylogenetically, although they agree in morphological features.

Ocellularia inturgescens clusters with strong support with *Sarcographina cyclospora* (Fig. 2). This relationship is surprising since the two taxa have little in common in terms of morphological characters; both share a minutely grainy thallus caused by large, columnar clusters of calcium oxalate crystals, but whereas *O. inturgescens* has small, rounded, myriotrema-like ascomata, those of *S. cyclospora* are lirellate and clustered in pseudostromatic areas (Fig. 4). Also, *O. inturgescens* has large, hyaline ascospores while they are small and dark brown in *S. cyclospora*. Given further the long branches leading to both taxa, it appears that this clade may represent a relict clade that included morphologically intermediate species which are now extinct (or have not yet been discovered).

The genera *Fibrillithecis*, *Myriochapsa*, and *Myriotrema* s.str. are strongly supported as monophyletic clades, sharing densely corticate thalli producing mostly psoromic acid and small, hyaline ascospores. They differ chiefly in ascomata features, with *Fibrillithecis* and *Myriochapsa* having erumpent to prominent ascomata with either fibrils (*Fibrillithecis*) or chroodiscoid lobules (*Myriochapsa*), and *Myriotrema* s.str. having small, rounded pores with double margin. The two specimens previously identified as *Fibrillithecis gibbosa* (H. Magn.) Rivas Plata & Lücking in Rivas Plata *et al.* (2010: 84) do not cluster together. Revision of the material revealed that only one corresponds to *F. gibbosa* s.str., whereas the other agrees with *F. platyspora* (Harm.) Frisch in Frisch *et al.* (2006: 137). At present we are unable to explain why *Myriotrema microporum* falls outside *Myriotrema* s.str., with a supported sister group relationship to *Myriochapsa* plus *Myriotrema* s.str. *Myriotrema microporum* agrees with *M. olivaceum*, the type of *Myriotrema*, in morphology, but produces psoromic instead of olivaceic acid. There is also an additional unsupported clade formed by a specimen similar to *M. microporum* and by *Fibrillithecis* aff. *sprucei* Mangold, Lücking & Lumbsch in Lumbsch *et al.* (2011: 55). Apparently, the latter is not a genuine *Fibrillithecis* and differs from *Fibrillithecis* s.str. in the large, muriform ascospores; this taxon might also deserve separate taxonomic status.

The genera *Compositrema* and *Stegobolus* form an unsupported sister group relationship, which agrees with their general similarities in morphology (Rivas Plata *et al.* 2012b; Mercado-Díaz *et al.* 2014). In fact, two species of *Compositrema*, *C. thailandicum* Rivas Plata *et al.* (2012b: 1174) and *C. borinquense* Mercado-Díaz *et al.* (2014), strongly resemble species of *Stegobolus* and would have been placed in that genus without molecular sequence data. Within *Compositrema*, our analysis clarified the identification of a specimen from Venezuela as identical with the newly described *C. isidiofarinosum* Mercado-Díaz *et al.* (2014) from Puerto Rico. It is also interesting to note that the only paleotropical species of *Compositrema* known so far is sister to a clade containing the three neotropical species, indicating a strong geographic signal. Within *Stegobolus*, it appears that specimens identified as *S. berkeleyanus* Montagne (1845: 4) from Australia (Mangold *et al.* 2009; as *Ocellularia*) do not represent that taxon, but are phylogenetically distinct.

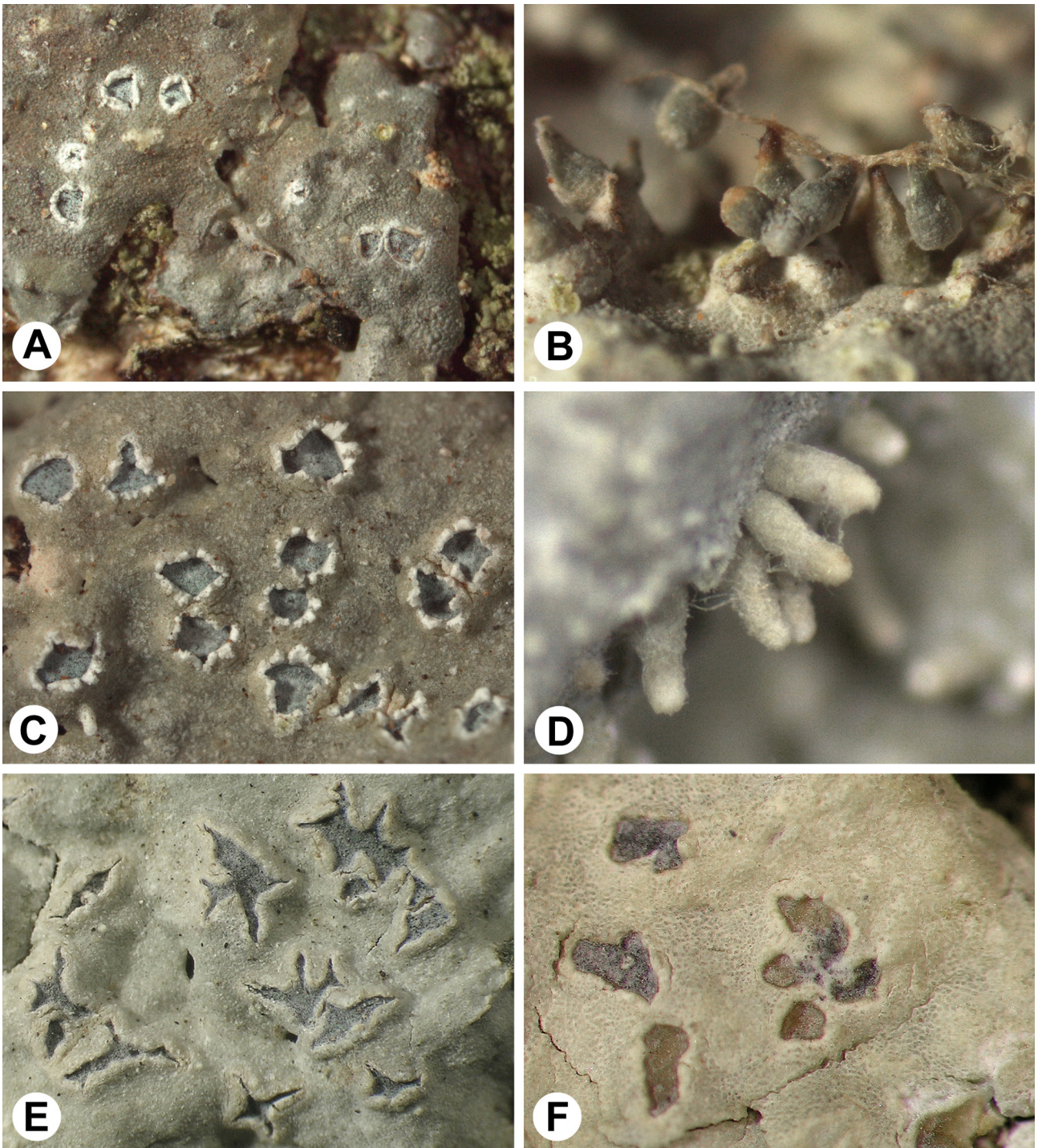


FIGURE 3. A–B. *Reimnitzia* aff. *santensis*, thallus with ascomata and isidia enlarged (India, *Lumbsch 19706b*). C. *Reimnitzia santensis*, thallus with ascomata (Florida, *Nelsen s.n.*). D. *Reimnitzia santensis*, isidia enlarged (Argentina, *Michlig et al. 106*). E. *Reimnitzia* aff. *santensis*, thallus with ascomata (Costa Rica, *Dodge 6633*). F. *Reimnitzia* aff. *santensis*, thallus with ascomata (Sri Lanka, *Weerakoon 305A*).

The genus *Redingeria* now includes three species with strong support with very different morphology. While *R. microspora* (Zahlbr.) M. Cáceres & Lücking in Cáceres *et al.* (2012: 809) features rounded ascomata, those of the newly described *R. desseiniana* Van den Broeck *et al.* (2014) and of *R. glaucoglyphica* (Sipman) Frisch in Frisch *et al.* (2006: 409) are elongate-lirellate. The inclusion of *R. desseiniana* in this genus is somewhat surprising, as this species closely resembles the genus *Phaeographopsis* Sipman in Aptroot *et al.* (1997: 129), which is not closely related (Lumbsch *et al.* 2014), in the farinose thallus, eolumellate lirellae, and dark brown, 3-septate ascospores (Fig. 5).

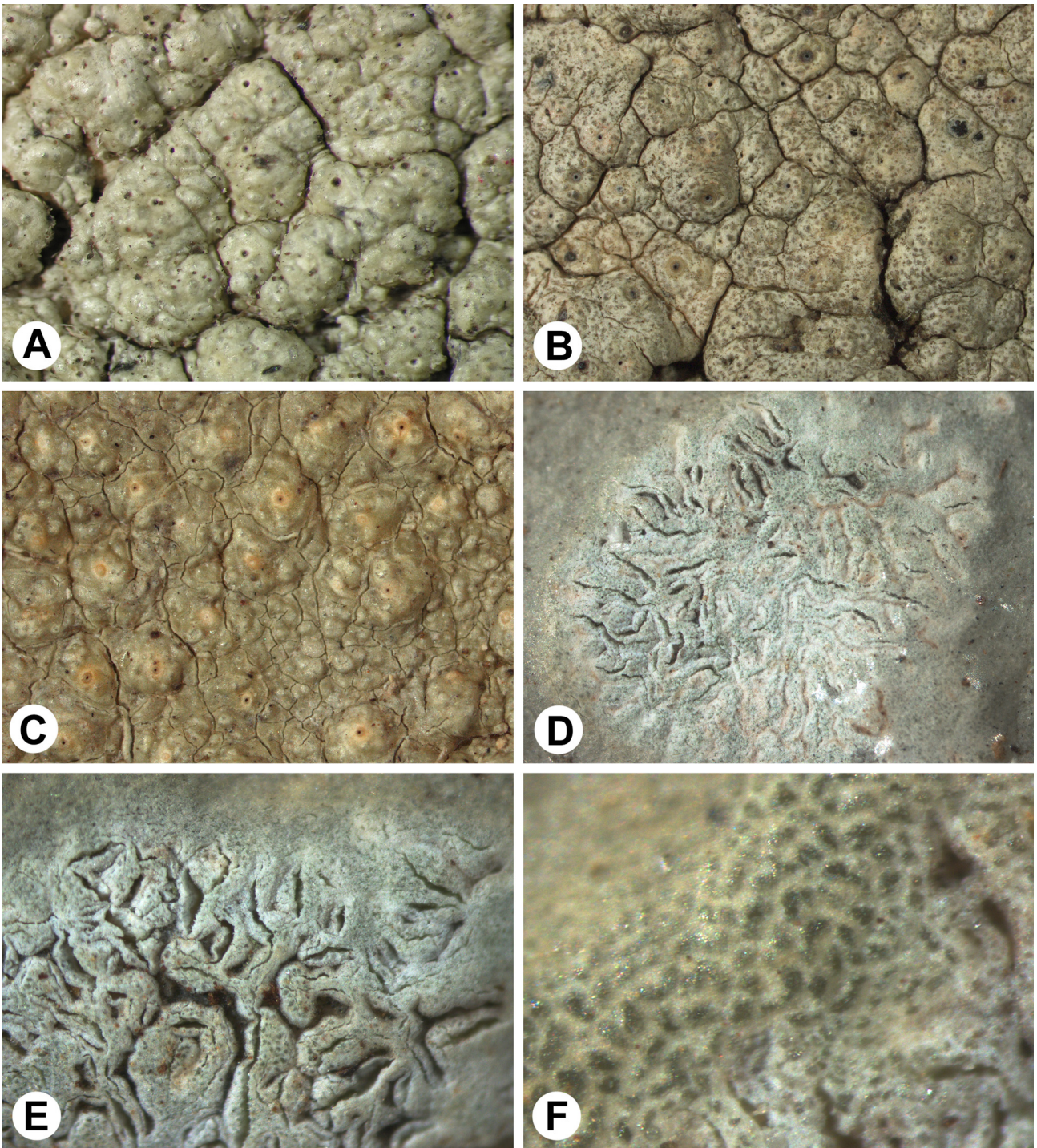


FIGURE 4. A–C. *Ocellularia inturgescens*, thallus with ascomata (A, holotype; B, Australia, *Brownlie A82c*; C, Australia, *Tibell 12788*). D–F. *Sarcographina cyclospora*, pseudostromatic ascomata and thallus surface enlarged (isotype).

Apart from *Myriotrema* s.str., there is a second clade centered around *Myriotrema album*, which is apparently not closely related. It presumably has the generic name *Ocellis* Clements (1909: 80, 175) available (Rivas Plata *et al.* 2012b). That name was introduced as new genus by Clements (1909), without giving a type but with a valid diagnosis "*Ocellularia didymospora*" (Clements 1909: 175), meaning *Ocellularia* species with 2-celled ascospores (ICN Art. 38.2). Since citing a type is only required from 1. January 1958 onwards (ICN Art. 40.1), the name *Ocellis* Clem. would be valid. However, the name coincides with a technical term (Latin: *ocellis* = dative and ablative plural of *ocellus* = eye) and hence, even if it was published before 1. January 1912, it is invalid since no species was cited in the protologue in combination with this name (ICN Art. 20.2). The citation of the type species as either *Ocellis myriopora* (Tuck.) Müll. Arg. [MB #431880] or *O. myriopora* (Tuck.) Clem. in Frisch *et al.* (2006:

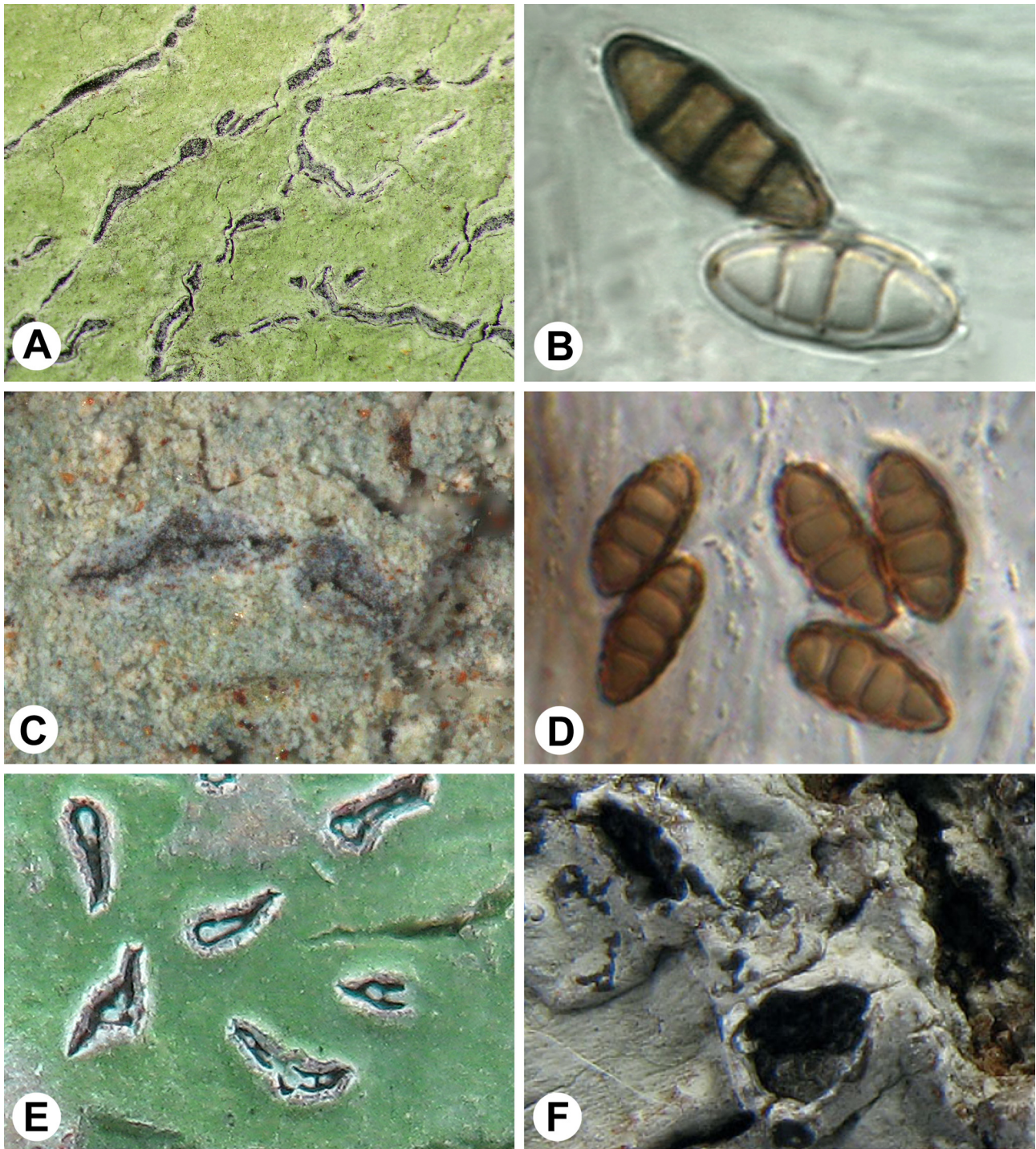


FIGURE 5. A–B. *Phaeographopsis neotropica*, thallus with ascomata and ascospores (Costa Rica, Lücking 16235a). C–D. *Redingeria desseiniiana*, ascomata and ascospores (holotype). E. *Redingeria glaucoglyphica*, thallus with ascomata (Peru, Rivas Plata 802A). F. *Redingeria microspora* (Brazil, Cáceres 6030).

166) and Mangold *et al.* (2009: 261) is incorrect, since neither Müller nor Clements made that combination and Clements (1909) did not even cite the species known at the time as *Ocellularia myriopora* (Tuck.) Müller (1888: 114). As a consequence, the *Myriotrema album* clade will eventually require the description of a new genus.

Ocellularia praestans forms an unsupported sister group relationship with *O. profunda* and relatives. We revised the taxonomy of specimens previously identified as *Ocellularia profunda* in the latter clade. The clade contains in fact four distinct taxa: *O. profunda* s.str., *O. kalbii* Mangold *et al.* (2007: 198), which differs from *O. profunda* in the lack of secondary substances, and two undescribed species, one with sorediate dactyls considered a variation of *O. profunda* (Mangold *et al.* 2009) and one with a sterile, strongly irregular thallus.



FIGURE 6. Best-scoring maximum likelihood tree of tribe Ocellularieae based on a 3-locus dataset, showing the *Rhabdodiscus* clade and the basal portion of *Ocellularia* s.lat. Supported branches are marked by thick lines and both bootstrap support values (70% or higher) and posterior probabilities (0.95 or higher) are given.

The strongly supported genus *Rhabdodiscus* comes out consistently as sister (Fig. 6) to *Nitidochapsa* plus *Ocellularia* s.lat. (Rivas Plata *et al.* 2013). Although generally with low support, *Rhabdodiscus* contains several newly described and yet unidentified species, such as *R. neocaledonicus* Papong *et al.* (2014), *R. saxicola* Papong *et al.* (2014), and *R. thouvenotii* Papong *et al.* (2014) from New Caledonia. Apparently this genus is richer in species than previously assumed and also includes species that deviate from the common pattern of olive-green, epiphytic thalli containing psoromic acid, as two of the New Caledonian species deviate in substrate (saxicolous) and chemistry.

Within the large *Ocellularia* s.lat. clade, the *O. terebrata* clade falls outside the strongly supported remainder of this group (Fig. 6), suggesting that the *O. terebrata* clade is another basal branch, next to *Rhabdodiscus*, of this species-rich lineage which contains the bulk of extant tropical species of this tribe. Our analysis suggests that specimens identified as *O. psorbarroensis* Sipman in Sipman *et al.* (2012: 145) in this clade may represent two phylogenetically distinct taxa. We also propose the new name ***Ocellularia hernandeziana* Kraichak, Lücking & Lumbsch, nom. nov.** [Mycobank #807665] for *Myriotrema ecorticatum* Lücking, J.E. Hern. & Kalb in Lücking *et al.* (2012: 4), non *O. ecorticata* Mangold in Mangold *et al.* (2009: 656)]. The non-monophyly of the newly described species *O. rondoniana* Cáceres *et al.* (2014) is due to missing data in the supermatrix on which our phylogenetic analysis was based. In this example, two of the three specimens have short mtSSU sequences whereas the third has nearly complete mtSSU and nuLSU data. The mtSSU sequences are identical in all three specimens except for different length, but since the short sequences cover a more conserved portion of the mtSSU, the analysis does not cluster all three specimens together, since mtSSU distances in this portion of the clade are generally short.

The *Ocellularia wirthii* clade was already recognized in previous analyses (Rivas Plata *et al.* 2012b, 2013) but is here recovered for the first time with strong support (Fig. 6), including besides *O. wirthii* also the newly described species *O. australiana* Mangold, Lücking & Lumbsch in Mangold *et al.* (2014) and *O. fuscosporella* Papong, Lücking & Lumbsch in Papong *et al.* (2014). Whereas *O. australiana* is similar to *O. wirthii* in most aspects, *O. fuscosporella* differs in ascoma morphology, chemistry, and especially in ascospore type. This illustrates that some of the phylogenetically defined and supported clades have few or none phenotypic synapomorphies that could be used to circumscribe the clade as a whole. On the other hand, the fact that all three species are known from a narrow area in tropical Australasia suggests regional radiations within Ocellularieae that in some cases evolved quite distinctive phenotypes, often in parallel to unrelated clades.

An unsupported clade within *Ocellularia* s.lat. includes *O. subpraestans* (Hale) Hale (1980: 138) sister to a supported clade comprising the newly described *O. austropacifica* Papong, Lücking & Lumbsch in Papong *et al.* (2014), *O. baileyi* s.lat., ***O. curranii* (Vain.) Kraichak, Lücking & Lumbsch, comb. nov.** [Mycobank #809094; *Thelotrema curranii* Vain., *Ann. Acad. Sci. Fenn., Ser. A*, 15(6): 186. 1921], and *O. allosporoides* (Nyl.) Patwardhan & Kulkarni (1977: 5) plus a close, undescribed relative of the latter lacking secondary substances (Fig. 6). This clade is of interest as it includes species with norisonotatic acid chemistry, underlining the importance of secondary chemistry in predicting phylogenetic relationships (Lumbsch *et al.* 2014). *Ocellularia austropacifica* is quite different from specimens identified as *O. baileyi* with salmon-pink medulla in both morphology and chemistry (no substances versus norisonotatic acid and pink pigment; Fig. 7). Hence, the close relationship, suggesting even possible conspecificity, comes as a surprise. Revision of the sequenced specimens labeled *O. baileyi* revealed that all of them feature a white medulla, suggesting that they might do not represent *O. baileyi* s.str. as indicated by Mangold *et al.* (2009), who accepted the latter as being variable in medulla color. The type of *O. baileyi* also has wider pores of the ascumata (Fig. 7). Due to missing sequences, the available sequence data are not sufficient to resolve the relationship between *O. austropacifica* and *O. aff. baileyi* (Fig. 8A): while mtSSU is practically identical in all specimens, nuLSU data show that *O. austropacifica* has ten synapomorphies compared to *O. aff. baileyi* (Fig. 8). However, since only one nuLSU sequence is available for that taxon, the other specimens will not be resolved correctly. This is comparable to the case of *O. allosporoides*, where specimens with norisonotatic acid (*O. allosporoides* s.str.) are not well-separated from those lacking substances (*O. aff. allosporoides*). Also here, nuLSU sequence data suggest grouping of the chemically different specimens into two clades corresponding to chemistry (Fig. 8B), but since three specimens are only represented by mtSSU data, phylogenetic analysis using a supermatrix approach does resolve this relationship.

The *Ocellularia massalongoi* clade includes *O. interposita* (Nyl.) Hale (1980: 137), *O. massalongoi* (Mont.) Hale (1980: 137), and *O. microstoma* (Müll. Arg.) Mangold *et al.* (2009: 324) and relatives (Fig. 9). All produce

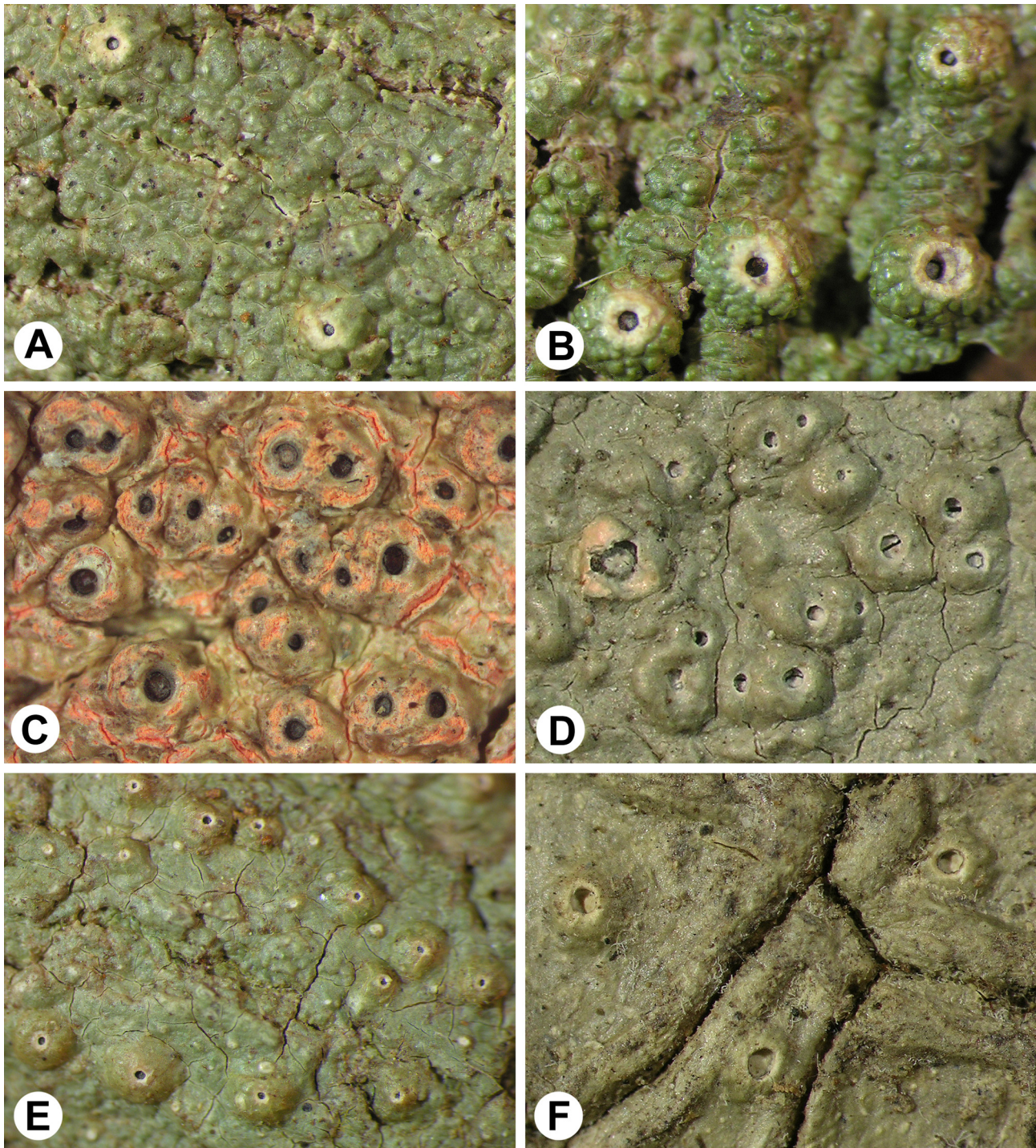


FIGURE 7. A–B. *Ocellularia austropacifica*, thallus with ascospores (A, isotype; B, paratype). C–D. *Ocellularia* cf. *baileyi*, thallus with ascospores (C, Australia, Tibell 15364; D, Australia, Kalb 34261). E. *Ocellularia* aff. *baileyi*, thallus with ascospores (New Caledonia, Papong 7982). F. *Ocellularia baileyi*, thallus with ascospores (isotype).

large, muriform ascospores but have variable chemistry including the psoromic, salazinic, and protocetraric acid chemosyndromes. Surprisingly, two species with small, dark brown ascospores are also supported in this clade, the newly described *O. pulchella* Lücking, Lumbsch & Parmen in Papong *et al.* (2014) and a specimen from Australia previously identified as *O. bahiana* (Mangold *et al.* 2009). Both otherwise resemble species of the *O. bahiana* clade in thallus structure, ascospores, and chemistry, and would have been expected to cluster within that clade instead. Specimens hitherto identified as *Ocellularia microstoma* (Rivas Plata *et al.* 2012b, 2013) come out in three separate clades, one with specimens from Japan, one with a single specimen from the Philippines, and five

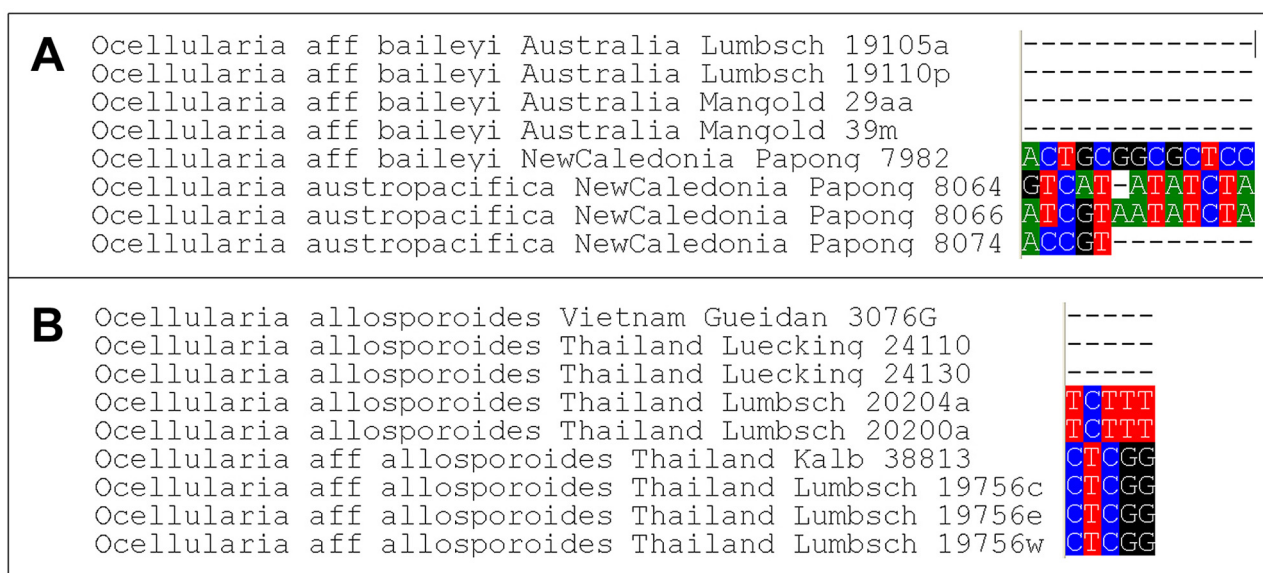


FIGURE 8. Screen shots from BIOEDIT of homologous columns of variable portions of the nuLSU for the clade containing *Ocellularia austropacifica* and *O. aff. baileyi* (above), as well as *O. allosporoides* and *O. aff. allosporoides* (below). In both cases, the species are distinguished by obvious synapomorphies in the nuLSU, but because mtSSU is practically identical between the species in each clade, specimens with mtSSU data alone cannot be resolved.

from the Philippines and Australia with two specimens from New Caledonia identified as *O. khasiana* (Patw. & Nagarkar) Kraichak, Lücking & Lumbsch, *comb. nov.* [Mycobank #807661; *Thelotrema khasianum* Patw. & Nagarkar, *Biovigyanam* 6: 8. 1980]. *Ocellularia khasiana* agrees with *O. microstoma* except for the chemistry, with protocetraric acid as main compound, whereas *O. microstoma* produces fumarprotocetraric acid, with protocetraric acid as accessory substance. Apparently, this minor chemical difference translates into phylogenetically distinct taxa. Since the type of *O. microstoma* is from Japan, we rechecked the chemistry of the Philippine and Australian specimens and found that they contain protocetraric acid as main compound. Notably, *O. cinerea* (Müll. Arg.) Kraichak, Lücking & Lumbsch, *comb. nov.* [Mycobank #807662; *Thelotrema cinereum* Müll. Arg., *Flora* 74: 112. 1891], which was included in *O. microstoma* by Mangold *et al.* (2009), is also a distinct species. It agrees with *O. microstoma* in producing fumarprotocetraric acid as main compound, but has smaller ascomata lacking a broad, flattened top and a light red-brown excipulum (dark brown in *O. microstoma*). The combination *Ocellularia microstoma* was accidentally introduced by Mangold *et al.* (2009), ascribing it to Hale (1980: 134). However, this is an erroneous citation, since Hale (1980: 134) cited the species as *Myriotrema microstomum* (Müll. Arg.) Hale. Nevertheless, the combination is valid and must be ascribed to the publication authors, viz. Mangold, Elix & Lumbsch.

No new data were obtained for the strongly supported *Ocellularia bahiana* clade (Fig. 9), except the finding that two species with phenotype features consistent with that clade fall into the *O. massalongoi* clade (see above). Two species within the *O. bahiana* clade require combination into *Ocellularia*: *O. erodens* (R. C. Harris) Kraichak, Lücking & Lumbsch, *comb. nov.* [Mycobank #807663; *Myriotrema erodens* R. C. Harris, *Some Florida Lichens*: 89. 1990] and *O. laeviuscula* (Nyl.) Kraichak, Lücking & Lumbsch, *comb. nov.* [Mycobank #807664; *Thelotrema laeviusculum* Nyl. in Triana & Planchon, *Ann. Sci. Nat. Bot., Ser. 4*, 19: 335. 1863; *Myriotrema laeviusculum* (Nyl.) Hale, *Mycotaxon* 11: 134. 1980]. *Ocellularia erodens* and *O. auberianoides* (Nyl.) Müller (1891b: 395) are closely related; both produce soralia and only differ in ascospore size. Whether the sterile, sorediate material here identified as *O. erodens* represents that species or sterile forms of *O. auberianoides* cannot be said with the data at hand, since the resolution provided by mtSSU and nuLSU sequence data might be insufficient in this case.

The strongly supported *Ocellularia perforata* clade (Fig. 9) consistently comes out as supported sister to *Myriotrema clandestinum*, seemingly providing another example of a *Myriotrema* species that requires recombination into *Ocellularia*. However, since the species with small, hyaline ascospores and psoromic acid have a very complex taxonomy and ascoma morphologies ranging from myriotremoid to ocellularioid, we prefer to

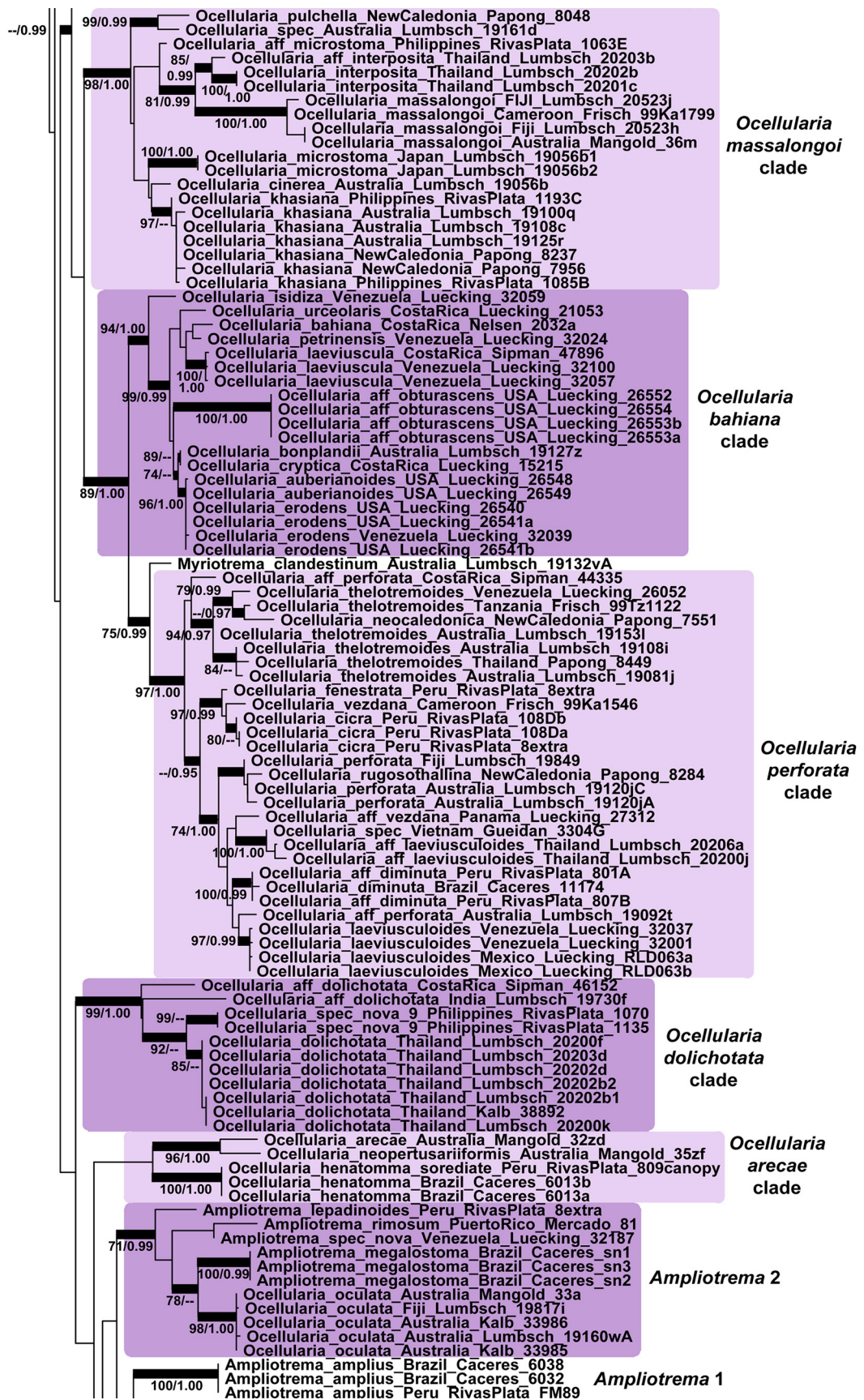


FIGURE 9. Best-scoring maximum likelihood tree of tribe Ocellularieae based on a 3-locus dataset, showing the central portion of *Ocellularia* s.lat. Supported branches are marked by thick lines and both bootstrap support values (70% or higher) and posterior probabilities (0.95 or higher) are given.

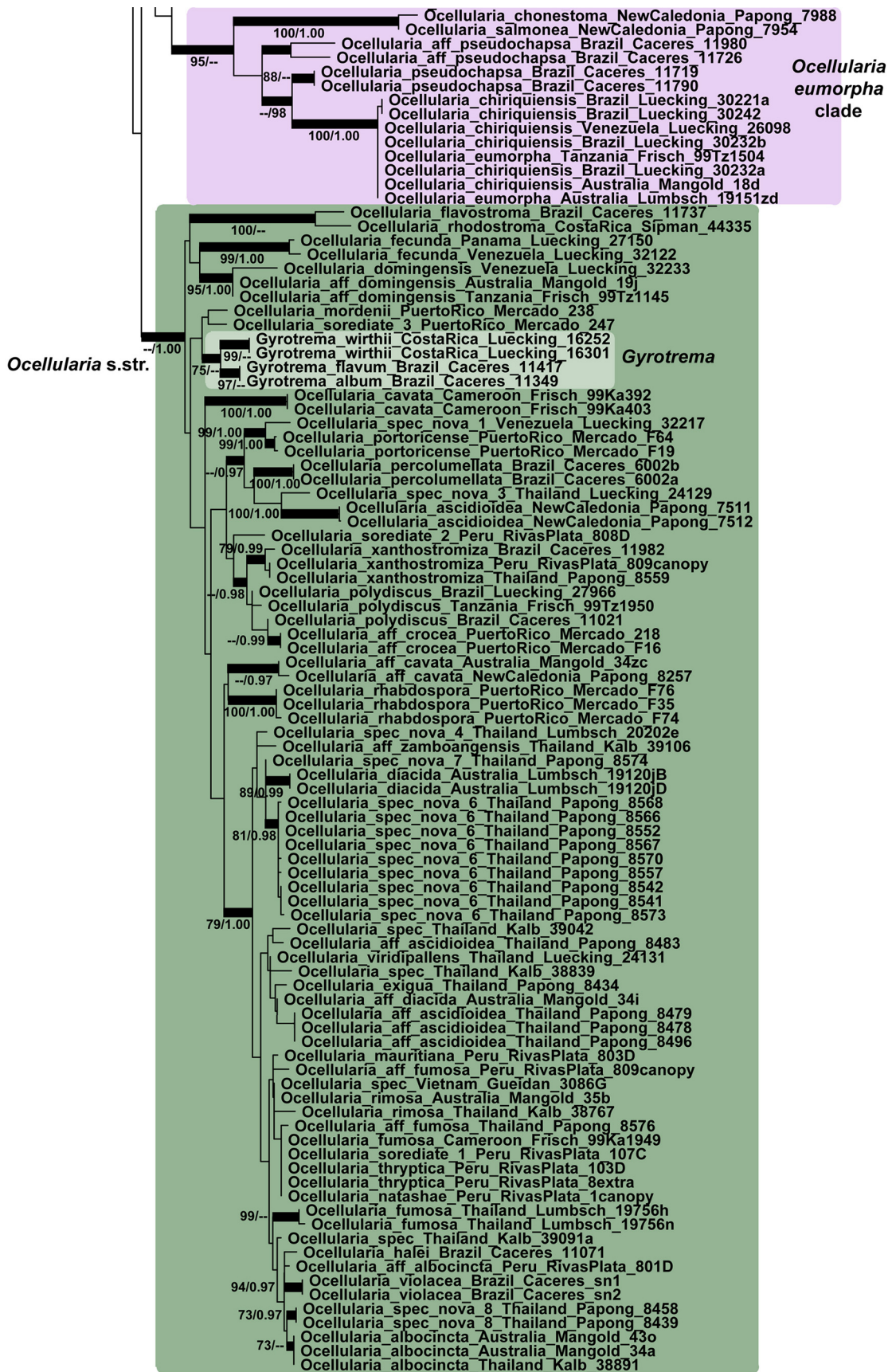


FIGURE 10. Best-scoring maximum likelihood tree of tribe Ocellularieae based on a 3-locus dataset, showing the terminal portion of *Ocellularia* s.lat. Supported branches are marked by thick lines and both bootstrap support values (70% or higher) and posterior probabilities (0.95 or higher) are given.

await further material of *Myriotrema clandestinum* to confirm the position of this species. It is possible that there are several, very similar taxa representing both genuine *Myriotrema* and *Ocellularia* species and hence recombining *M. clandestinum* in *Ocellularia* appears premature. Within the *O. perforata* clade, there are two further examples of unresolved, complex species-level phylogenies. Thus, the topology for material identified as *O. thelotremoides* (Leight.) Zahlbruckner (1923: 603) suggests that more than one species are involved, particularly because the newly described species *O. neocaledonica* Lücking, Lumbsch & Parmen in Papong *et al.* (2014), is nested on a long branch within the *O. thelotremoides* complex, even if it is morphologically and chemically distinct. While *O. thelotremoides* has submuriform ascospores and protocetraric acid, *O. neocaledonica* has 5-septate, smaller ascospores and lacks secondary substances. Notably, the specimens identified as *O. thelotremoides* cluster according to their geographical distribution, further supporting the hypothesis that these represent at least three distinct taxa. Likewise, *O. rugosothallina* Lücking, Lumbsch & Parmen in Papong *et al.* (2014) is nested on a long branch within the *O. perforata* complex. These species complexes, including also *O. papillata* (Leight.) Zahlbruckner (1923: 597) and *O. terebrata*, require further study with ample material from throughout the tropics.

The backbone of the remainder of *Ocellularia* s.lat. (Fig. 9, 10), including *Ocellularia* s.str. centered around *O. cavata* (Ach.) Müller (1882: 499), is not supported; hence this analysis does not allow any new conclusions about the position of the genera *Ampliotrema* and *Gyrotrema* (Rivas Plata *et al.* 2012b). As in our previous analysis, *Ampliotrema* forms two clades, one containing the type species, *A. amplius*, and the other comprising all other species. *Ampliotrema amplius* is unsupported sister to the *O. eumorpha* clade, which also contains *O. chonestoma* (Leight.) Zahlbruckner (1923: 586) and the newly described *O. salmonea* Lücking, Lumbsch & Parmen in Papong *et al.* (2014) and *O. pseudochapsa* M. Cáceres, Aptroot & Lücking in Cáceres *et al.* (2014). The polyphyly of *Ampliotrema* must be studied further: the genus appears monophyletic based on mtSSU sequence data, whereas the single available nuLSU sequence for one of the three specimens of *A. amplius* clusters with *O. eumorpha* and relatives. Notably, the undescribed taxon resembling *O. pseudochapsa*, but with corticate thallus (Cáceres *et al.* 2014), also falls within this clade but represents a distinct species.

Several other newly described and undescribed species are found in this portion of the tree, particularly within the supported *Ocellularia* s.str. clade (Fig. 10), which appears to contain the largest number of species among the clades currently classified in *Ocellularia*. *Ocellularia* s.str. includes many taxa with pigmented medulla and the cinchonarum unknown chemistry, although protocetraric and hypoprotocetraric acid are also frequent. Some preliminary conclusions can be drawn about the *O. cavata* complex. Currently, this name includes all material with smooth to verrucose thallus, carbonized, columellate ascomata, small to medium-sized, transversely septate, hyaline ascospores, a pale yellow to orange medulla, and the cinchonarum unknown chemistry (Frisch *et al.* 2006; Mangold *et al.* 2009). Although very few specimens with these characters have been sequenced, they form several, only distantly related clades. Thus, *O. cavata* from tropical Africa (Cameroon) is phylogenetically distinct from specimens with similar features collected in Australia and New Caledonia. Specimens with distinctly verrucose thallus form a separate clade here identified with *O. xanthostromiza* (Nyl.) Zahlbruckner (1923: 604), previously considered a synonym of *O. cavata*. Notably, this is thus far the only confirmed case of a rain forest understory species of this tribe to have a pantropical distribution, known from Peru, Brazil, and Thailand. Other material from Thailand with comparatively small ascomata forms another clade corresponding to a yet undescribed species (spec. nova 6). Also *O. polydiscus* Redinger (1933: 61) differs from *O. cavata* in the complex columella, and *O. aff. crocea* (Kremp.) Overeem & Overeem in Overeem (1922: 118), differing from *O. cavata* in a fissured ascoma margin. These very preliminary data suggest that *Ocellularia* is one of the genera where both future inventories and an increased amount of molecular data will lead to the recognition of many more species than currently accepted.

Conclusions

The updated phylogenetic analysis of tribe Ocellularieae supported earlier findings and also exhibits consistent placements of some of the clades even with lack of support. Thus, a broader picture of the evolution and classification of this tribe is emerging. However, some clades remain undersampled, in particular those containing species currently classified in *Ocellularia* but falling outside *Ocellularia* s.lat. Species of these clades must be primary targets for gathering further sequence data, in order to better understand the phenotype features that

characterize these clades and eventually give them formal generic status. In addition, it becomes apparent that, at least in this clade, nuLSU and also *RPB2* provide a better resolution at species and species group level than mtSSU; on the other hand, the proportion of sequences routinely obtained for taxa within this clade indicates that nuLSU and particularly *RPB2* sequencing often fails. The highlighted cases suggest that especially within *Ocellularia* s.lat., additional data from these two loci may help to better resolve this clade and then either define subgenera or even additional genera.

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