

Emmanuelia, a new genus of lobarioid lichen-forming fungi (*Ascomycota: Peltigerales*): phylogeny and synopsis of accepted species

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Abstract. The former family *Lobariaceae*, now included in *Peltigeraceae* as subfamily *Lobarioideae*, has undergone substantial changes in its generic classification in recent years, based on phylogenetic inferences highlighting the polyphyly of the speciose genera *Lobaria*, *Pseudocyphellaria* and *Sticta*. Here we introduce the new genus *Emmanuelia*, named in honor of Prof. Emmanuël Sérusiaux for his extensive work on the *Peltigerales*. *Emmanuelia* currently comprises twelve species. It is superficially similar to the lobarioid genus *Ricasolia*, but differs by its apothecia, rimmed by overarching and often crenulate to lobulate margins, with the parathecium (proper excipulum) and the amphithecium (thalline excipulum formed by the thallus cortex) apically separated and of a different structure. Also, ascospore dimensions and shape differ between the two genera, with the ascospores of *Emmanuelia* being longer and narrower. Molecular phylogenetic analyses using DNA nucleotide sequences of the internal transcribed spacer region (ITS) and the small subunit of mitochondrial ribosomal DNA (mtSSU) confirm that *Emmanuelia* belongs to the *Lobaria* s.lat. clade and forms a monophyletic group sister to the lineage consisting of *Dendriscosticta*, *Lobariella* and *Yoshimuriella*. None of the available generic names of lobarioid lichens can be applied to this group, and consequently a new name is proposed for this new genus, which is typified with *E. ravenelii* comb. nov. Eleven other species are transferred to *Emmanuelia*: *E. americana* comb. nov., *E. conformis* comb. nov., *E. cuprea* comb. nov., *E. elaeodes* comb. nov., *E. erosa* comb. nov., *E. excisa* comb. nov., *E. lobulifera* comb. nov., *E. ornata* comb. nov., *E. patinifera* comb. nov., *E. pseudolivacea* comb. nov. and *E. tenuis* comb. nov. The genus is represented in North America by three species, including *E. lobulifera*, which is resurrected from synonymy with *E. (Lobaria) tenuis*, a South American species, and *E. ornata*, whose populations were previously treated under *E. (Lobaria) ravenelii*.

Key words: Brazil, *Dendriscoaulon*, *Lobarioideae*, Neotropics, *Peltigeraceae*, *Ricasolia*, taxonomy, USA

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Introduction

Recent years have witnessed major systematic rearrangements of lobarioid lichens. In less than a decade, the number of genera circumscribed in this lineage of conspicuous macrolichens was multiplied by four. Essentially, the three long-established genera (*Lobaria*, *Pseudocyphellaria*, *Sticta*), which were diagnosed by single morphological features (the presence/absence of cyphellae or pseudocyphellae), did not survive the advent of molecular phylogenetics and were partitioned into twelve genera (Galloway & Elix 2013; Moncada et al. 2013; Galloway 2015; McCune et al. 2014). As an example, moon lichens, which were characterized by the presence of crater-like pores on the lower cortex, are no longer considered as a monophyletic group under the genus name *Sticta*, as this trait evolved in two unrelated lineages. Thus, the genus *Dendriscosticta*, more closely related to *Lobaria*, was introduced to accommodate the additional lineage (Moncada et al. 2013).

In addition to the profound changes in generic concepts, lobarioid lichens were not spared from a recent systematic revision at the family level: in a recent study by Kraichak et al. (2018), under a temporal-banding proposal (Avisé & Johns 1999; Kraichak et al. 2017), the authors proposed treating the families *Lobariaceae* and *Nephromataceae* as synonyms of *Peltigeraceae*. While the mechanistic approach of temporal banding classifications has been criticized, the broad agreement in morphological, anatomical and chemical features and the absence of a clear diagnostic character for each of the three previously separated families justifies this revised classification (Lücking 2019). As a consequence, lobarioid lichens, long treated as *Lobariaceae*, are now recognized as members of the subfamily *Lobarioideae* within *Peltigeraceae* (Lumbsch & Leavitt 2019).

In the present study, yet another new genus, *Emmanuelia*, is erected to accommodate a group of lobarioid lichens that cannot be placed in any of the existing genera. The species of interest belong to a lineage mostly restricted to the Neotropics and the southeastern United States, and were previously treated as members of the genus *Lobaria* and subsequently considered part of *Ricasolia* (Moncada et al. 2013; Kaffer et al. 2016; Lehnen et al. 2017; Etayo et al. 2018). Yoshimura (1998) treated the South American taxa as *L. quercizans* group, also implying a close relationship to *Ricasolia*. This group of lichens includes, among others, shade-loving species of the Atlantic Forest biome in South America such as *L. tenuis* (Kaffer et al. 2009), as well as *L. ravenelii*, a well-known taxon characteristic of the Atlantic–Gulf Coastal Plain in North America (Jordan 1973). To address their phylogenetic affinity, we reconstructed the phylogeny of the *Lobaria* s.lat. clade by using sequence data of two loci obtained from seven related genera of *Lobarioideae*. Our molecular analysis confirmed that *L. ravenelii* and other related species should be accommodated in a new segregated genus of *Lobaria* s.lat.

Material and methods

Taxon sampling and phenotypic characterization

The present study is based on detailed examination of lichen specimens provided by NY (William and Lynda Steere Herbarium, New York, USA) and numerous freshly collected specimens from fieldtrips to Brazil, the Caribbean Islands and Galapagos Islands. Thirty-four representatives of the taxonomic group of interest were selected based on preliminary phylogenetic analysis of the internal transcribed spacer region (ITS), along with ten specimens from related genera. Morphological features were observed at various laboratories, using various dissecting microscopes (Olympus SZ60, Leica Zoom 2000) and compound microscopes (Olympus BX53, Nikon Eclipse 80i, Zeiss Axioskop). Secondary chemistry was investigated through thin-layer chromatography (TLC) using solvent G and following the protocol by Orange et al. (2001). Detailed descriptions were provided for the generic type of the newly introduced genus (*E. ravenelii*) and for the resurrected species (*E. lobulifera*). For all other species we added short diagnostic descriptions.

DNA extraction, amplification, and sequencing

Genomic DNA was isolated using Nucleospin Plant II Midi kits (Macherey-Nagel, Bethlehem, Pennsylvania, USA), following the manufacturer's guidelines or following the protocol by Cubero et al. 1999. We amplified and sequenced the internal transcribed spacer region (ITS) using primers ITS1F (Gardes & Bruns 1993) and ITS4 (White et al. 1990), and the small subunit of mitochondrial ribosomal DNA (mtSSU) using primers SSU1 and SSU3R (Zoller et al. 1999). Standard PCR protocols were carried out using GoTaq Green Master Mix (Promega, Madison, Wisconsin, USA), following the manufacturer's guidelines. The thermal cycling parameters were set as follows: 94°C for 3 min, followed by 35–40 cycles of 94°C for 1 min, 52°C for 1 min and 70°C for 1 min, with a final extension of 70°C for 10 min. The quality and size of the amplicons were visually checked on a 1% w/v agarose gel stained by SYBR Safe DNA Gel Stain (Thermo Fisher Scientific Inc., Waltham, Massachusetts, USA). Amplicons were cleaned using the ExoSAP-IT protocol (USB Corporation, Cleveland, Ohio, USA) and sequenced on a ABI Prism 3100 Genetic Analyzer (Applied Biosystems, Foster City, California, USA), or by Macrogen, Inc. (Seoul, South Korea). The forward and reverse sequences obtained were assembled and edited using Geneious 10.0.7 (Biomatters Ltd., Auckland, New Zealand) or Sequencher version 4.9 (Gene Codes Corporation, Ann Arbor, Michigan, USA). The resulting sequences were submitted to GenBank (Table 1).

Alignment and sequences analyses

The sequences generated for each gene were aligned with selected sequences from species of the *Lobaria* s.lat. clade from GenBank, using the genus *Sticta* as outgroup, in agreement with recent phylogenetic studies (e.g., Moncada et al. 2013; Widhelm et al. 2019; Table 1). The final

Table 1. GenBank numbers and voucher information for specimens and sequences used in this study. Newly generated sequences are bolded.

Species	ITS	mtSSU	Voucher	Origin
<i>Dendriscosticta</i> aff. <i>wrightii</i>	MT110113	MT110145	Goffinet 13074 (CONN)	Taiwan
<i>D. praetextata</i>	MT110112	MT110144	LS Wang, HX Shi 14-46246 (KUN)	China
<i>D. sp.</i>	MT110111	MT110143	Goffinet 13005 (CONN)	Taiwan
<i>Emmanuelia</i> aff. <i>elaeodes</i>	MT110106	MT110138	Mercado-Díaz 2939 (F)	Dominican Republic
<i>E. aff. elaeodes</i>	MT110082	–	Mercado-Díaz 3526a (F)	Jamaica
<i>E. aff. ravenelii</i>	MT110107	MT110139	Mercado-Díaz 3031 (F)	Dominican Republic
<i>E. aff. tenuis</i>	MT110089	MT110125	Lücking 37504 (B, JOI)	Brazil
<i>E. aff. tenuis</i>	MT110096	MT110132	Lücking 39705 (B, ISE)	Brazil
<i>E. americana</i>	MT110098	–	Lücking 40112 (B, JOI)	Brazil
<i>E. elaeodes</i>	MT110090	MT110126	Lücking 37511 (B, HAS)	Brazil
<i>E. elaeodes</i>	MT110091	MT110127	Lücking 37544a (B, HAS)	Brazil
<i>E. elaeodes</i>	MT110093	MT110129	Lücking 37546 (B, HAS)	Brazil
<i>E. elaeodes</i>	MT110099	–	Lücking 40082 (B, JOI)	Brazil
<i>E. elaeodes</i>	MT110087	MT110123	Spielmann 11214 (B, CGMS)	Brazil
<i>E. erosa</i>	MT110094	MT110130	Cáceres 25148 (B, ISE)	Brazil
<i>E. erosa</i>	MT110097	MT110133	Mercado-Díaz 3038c (F)	Dominican Republic
<i>E. lobulifera</i>	MT110076	–	Kaminski 18013 (NY)	USA, Florida
<i>E. lobulifera</i>	MT110100	–	Lendemmer 21578 (NY)	USA, Georgia
<i>E. lobulifera</i>	MT110108	MT110140	Lendemmer 41467 (NY)	USA, South Carolina
<i>E. lobulifera</i>	MT110075	–	Rosentreter 19739 (NY)	USA, Florida
<i>E. ornata</i>	MT110085	MT110121	Moncada 8401(B, CDS)	Ecuador, Galapagos
<i>E. ornata</i>	MT110086	MT110122	Moncada 8402 (B, CDS)	Ecuador, Galapagos
<i>E. ornata</i>	MT110109	MT110141	Rosentreter 17651 (NY)	USA, Florida
<i>E. ornata</i>	MT110074	–	Rosentreter 20233 (NY)	USA, Florida
<i>E. patinifera</i>	MT110101	–	Cáceres 25182 (B, ISE)	Brazil
<i>E. ravenelii</i>	MT110105	MT110137	Buck 63035 (NY)	USA, North Carolina
<i>E. ravenelii</i>	MT110102	MT110134	Lendemmer 34974 (NY)	USA, North Carolina
<i>E. ravenelii</i>	MT110103	MT110135	Quendensley 10852 (NY)	USA, Georgia
<i>E. ravenelii</i>	MT110104	MT110136	Tripp 4654 (NY)	USA, North Carolina
<i>E. tenuis</i>	MT110088	MT110124	Lücking 37502 (B, HAS)	Brazil
<i>E. tenuis</i>	MT110092	MT110128	Lücking 37544b (B, HAS)	Brazil
<i>E. tenuis</i>	MT110095	MT110131	Lücking 40067 (B, JOI).	Brazil
<i>Lobarina isidiosa</i>	MT110077	MT110114	LS Wang, HX Shi 14-46398 (KUN)	China
<i>L. isidiosa</i>	MT110078	MT110115	LS Wang, HX Shi 14-46417 (KUN)	China
<i>L. linita</i>	EU558809	AB239702	Högnabba et al. (2009), Takahashi et al. (2006)	–
<i>L. orientalis</i>	MT110080	MT110117	LS Wang, HX Shi 14-45557 (KUN)	China
<i>L. orientalis</i>	MT110079	MT110116	LS Wang, HX Shi 14-46123 (KUN)	China
<i>L. pulmonaria</i>	AF069541	AF129284	Zoller et al. (1999)	–
<i>L. retigera</i>	MT110081	MT110118	Goffinet 13103 (CONN)	Taiwan
<i>L. retigera</i>	AY124159	AY124094	Lohtander et al. (2002)	–
<i>L. sachalinensis</i>	EU558815	AF524906	Högnabba et al. (2009), Stenroos et al. (2003)	–
<i>Lobariella pallida</i>	DQ912296	HQ650695	Miadlikowska et al. (2006), Schmull et al. (2011)	–
<i>L. pallidocrenulata</i>	KC011075	KC011051	Moncada et al. (2013)	–
<i>L. reticulata</i>	KC011076	KC011063	Moncada et al. (2013)	–
<i>L. subcrenulata</i>	DQ912297	HQ650696	Miadlikowska et al. (2006), Schmull et al. (2011)	–
<i>L. subexornata</i>	EU558804	AF524902	Högnabba et al. (2009), Stenroos et al. (2003)	–
<i>Lobarina oregana</i>	MT110083	MT110119	Riley 7/20/04 DNA vouch. 4 (NY)	USA, Washington
<i>L. scrobiculata</i>	AY340506	AF350297	Wiklund & Wedin (2003), Thomas et al. (2002)	–
<i>L. silvae-veteris</i>	MT110084	MT110120	Goward 04-05 (UBC)	Canada
<i>Ricasolia amplissima</i>	AY340500	AF524923	Wiklund & Wedin (2003), Stenroos et al. (2003)	–
<i>R. virens</i>	MT110110	MT110142	Tønsberg 44757 (BG)	Norway
<i>Sticta sublimbata</i>	JQ736019	JQ735986	Magain et al. (2012)	–
<i>S. sylvatica</i>	KT281736	KT281692	Magain & Sérusiaux (2015)	–
<i>Yoshimuriella</i> aff. <i>subdissecta</i>	KC011073	KC011029	Moncada et al. (2013)	–
<i>Y. dissecta</i>	EU558808	AF524920	Högnabba et al. (2009), Stenroos et al. (2003)	–

dataset contained representatives of all known genera within the *Lobarina* s.lat. clade. Alignment for each gene was assembled in Geneious 10.0.7 (Biomatters Ltd., Auckland, New Zealand) pre-aligned using MAFFT run in auto mode (Katoh 2002; Katoh et al. 2009), and the

ends of each alignment were trimmed. The final matrices were obtained using default MAFFT settings, with two alignment iterations, as implemented in the Guidance Web Server (Penn et al. 2010a, b; Sela et al. 2015). Sites with low-quality scores (i.e., with confidence scores

below 0.93) reported by GUIDANCE 2 were excluded from the datasets, which resulted in alignments of 589 bp (initially 779 bp) and 700 bp (initially 941 bp) for ITS and mtSSU, respectively. As strongly supported topological conflicts were not observed when the loci were analyzed separately, the two markers were combined into a concatenated matrix of 1289 bp. The concatenated dataset included 55 terminals, all represented by ITS, and 47 of which were also represented by the mtSSU marker. PartitionFinder 2 (Lanfear et al. 2016) was used to determine the best partitioning schemes and nucleotide substitution models for the subsequent maximum likelihood (ML) analysis on the concatenated dataset. Two initial subsets were considered (ITS, mtSSU) and the default configuration settings were used (branchlengths = linked, models = GTR+G, model_selection = AICc) with the greedy algorithm (Lanfear et al. 2012) and PhyML (Guindon et al. 2010). An ML analysis was performed on the 2-gene dataset using RAxML-HPC2 8.2.12 (Stamatakis 2014) on the CIPRES portal (Miller et al. 2010; <https://www.phylo.org>), using the rapid hill-climbing algorithm and bootstrapping with 1000 pseudoreplicates under a GTR+G model of evolution for each subset provided by PartitionFinder 2 (subset 1: ITS; subset 2: mtSSU).

Relationships among the *Emmanuelia elaeodes* species aggregate (*E. americana*, *E. elaeodes*, *E. ravenelii*, *E. tenuis*) remained largely unresolved in our ML phylogenetic tree (Fig. 1A). For this reason, we constructed a haplotype network for these closely related species, using the TCS v1.21 program (Clement et al. 2000) as implemented in PopART software (Leigh & Bryant 2015). The ITS sequences of these species were re-aligned using the general MAFFT settings as implemented in the Guidance Web Server. Since the resulting alignment contained relatively few ambiguous portions, the dataset was loaded with all sites included. Sites with undefined states were then masked, and sequences containing significantly more undefined states than others were removed from the analysis.

Based on the 2-gene dataset, a strict molecular clock model was employed to date the evolutionary origin of the genus *Emmanuelia*, using the Bayesian program BEAST 1.10.4 (Drummond & Rambaut 2007). We initially conducted a run using a relaxed, log-normal, uncorrelated clock: this preliminary run supported a clock-like rate of evolution, as the standard deviation estimate of the clock (i.e., the 'ucl.d.stdev' parameter estimate) was close to zero. Consequently, a strict clock prior was applied. The dataset was analyzed with unlinked substitutions models across the two loci, and the most appropriate nucleotide substitution model for each locus was determined based on the AICc model selection criterion as implemented in jModelTest2 (Darriba et al. 2012) and using five substitution schemes (ITS: TrN+I+G; mtSSU: HKY+I+G). A Yule prior was assigned to the speciation process (Yule 1924; Gernhard 2008). The 'ucl.d.mean' prior (mean substitution rate) was set to a diffuse gamma distribution (shape 0.001, scale 1000). The time to the most recent ancestor ('tmrca') for the ingroup node (*Lobaria* s.lat. clade) was calibrated at 57.6 myr, using a normal prior distribution

with the standard deviation set to 13 myr; this calibration followed the results of the time-calibrated *Lobariaceae* phylogeny by Widhalm et al. (2019). All other priors were held to default values. The BEAST analysis was run for 50 million generations, sampling parameters every 5000 steps, and performed on the CIPRES Science Gateway (Miller et al. 2010). Convergence, mixing, and effective sample sizes (ESS) of parameters were checked in Tracer 1.6 (Rambaut et al. 2014). All ESS values were above 200. A burn-in of 10% was discarded from the run. A maximum credibility tree with a cut-off of 0.5 of posterior probabilities was generated with the remaining 9,000 trees in TreeAnnotator version 1.10.4 (BEAST package). The results of the ML and Bayesian analyses were visualized with the R package ggtree (Yu et al. 2017).

Results

Emmanuelia emerged as a strongly supported monophyletic group (ML bootstrap support [BS]=100, posterior probabilities [PP]=1) on a fairly long branch within the *Lobaria* s.lat. clade (Fig. 1A). In contrast, backbone support values within *Emmanuelia* were low, suggesting a rather recent radiation. *Emmanuelia* was recovered as sister to a clade consisting of *Dendriscosticta*, *Lobariella* and *Yoshimuriella* by both ML and Bayesian inferences, and not directly related to *Ricasolia*, justifying the introduction of a new genus to accommodate this group of lichenized fungi. Within *Emmanuelia*, strong support was obtained for a clade of four species: *E. americana*, *E. elaeodes*, *E. ravenelii* and *E. tenuis*. Relationships within this clade remained mostly unresolved under ML. The TCS haplotype network (Fig. 1B) for 13 specimens within the *E. elaeodes* species aggregate further highlighted the lack of signal in the ITS marker to segregate these species (with the exception of *E. ravenelii*, which appeared well-differentiated in both TCS and ML analyses).

The strict molecular clock analysis estimated the crown node age of the genus *Emmanuelia* at 10.2 myr in the late Miocene (95% high probability density [HPD]: 4.0–17.8 myr; Fig. 2). The stem node age of *Emmanuelia* versus its sister clade (*Dendriscosticta* + *Lobariella* + *Yoshimuriella*) was estimated at 29.8 myr in the early Oligocene (HPD: 11.1–48.2 myr).

Although *Ricasolia* is not directly related to *Emmanuelia*, it is morphologically most similar to the latter, whereas the related genera *Dendriscosticta*, *Lobariella* and *Yoshimuriella* are easily distinguished. Yet, analyses of morphological and anatomical characters revealed a number of subtle differences between *Emmanuelia* and *Ricasolia*. In *Emmanuelia* the apothecial margins are typically overarching and lobulate, with a rough outer surface, whereas in *Ricasolia* they are slightly prominent, more or less entire, and with a smooth outer surface. In *Emmanuelia* the parathecium (i.e., proper excipulum) appears to be apically separated from the amphithecium (i.e., thalline excipulum formed by the thallus cortex) by the photobiont layer which reaches up to the apex, and also different in structure (prosoplectenchymatous vs. paraplectenchymatous; Fig. 3A–B). In *Ricasolia* the

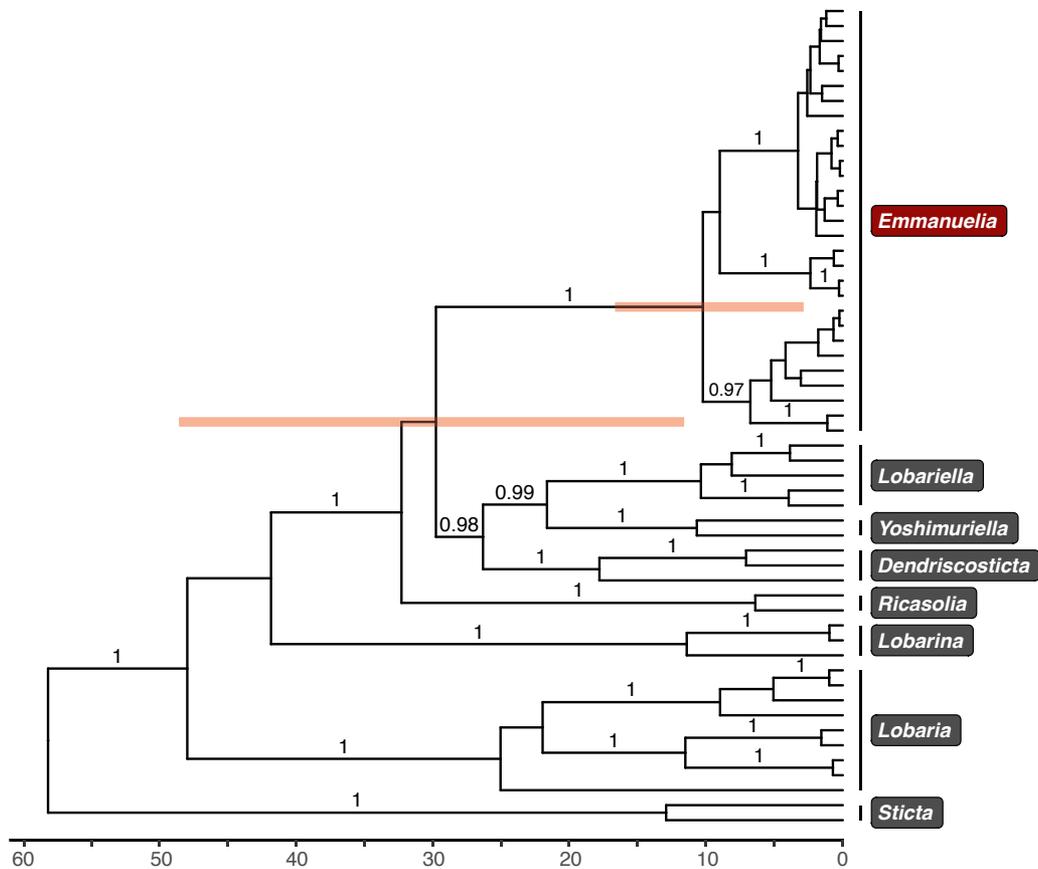


Figure 2. Strict molecular clock tree of the *Lobaria* s.lat. clade, showing origin and diversification of *Emmanuelia*. Red-brown bars indicate the 95% posterior density interval of crown and stem node age for the genus *Emmanuelia*. Values above branches represent posterior probabilities (indicated when greater than or equal to 0.95). Scale at bottom: millions of years before present.

sequenced species of *Emmanuelia* the following values were observed: $60\text{--}75 \times 2.5\text{--}3 \mu\text{m}$, $\sim 20\text{--}25$ times as long as broad (*E. ravenelii*), $60\text{--}80 \times 2\text{--}3 \mu\text{m}$, $\sim 20\text{--}30$ times as long as broad (*E. elaeodes*), $60\text{--}70 \times 3\text{--}3.5 \mu\text{m}$, $\sim 15\text{--}20$ times as long as broad (*E. tenuis*), and $50\text{--}80 \times 2.5\text{--}4 \mu\text{m}$, $\sim 17\text{--}22$ times as long as broad (*E. patinifera*). Somewhat similar measures, with length between 55 and $80 \mu\text{m}$, width between 3 and $4 \mu\text{m}$, and length/width ratio between 15 and 25, were reported in the literature for *E. americana*, *E. cuprea*, *E. pseudolivacea* and *E. tenuis* (e.g., Yoshimura & Osorio 1975; Fig. 4). Thus, while the overall variation between the two genera appears to be gradual, ascospores of *Emmanuelia* tend to be longer and relatively narrower than those of *Ricasolia*.

Discussion

Under two different tree-building strategies, the new genus *Emmanuelia* forms a well-supported monophyletic group restricted to the New World and sister to a lineage consisting of *Dendrioscoticta*, *Lobariella* and *Yoshimuriella*. This result, and the overall tree topology, agree with the phylogenomic analysis of the *Lobarioideae* (as *Lobariaceae*) by Widhelm et al. (2019). Their study and ours have in common three representatives of *Emmanuelia*. These shared samples are here referred to as *E. aff. elaeodes*, *E. aff. ravenelii* and *E. erosa* (Mercado-Díaz 2939, 3031,

3038c), and as *Ricasolia* spp. (15682, 15683, 15685) in Widhelm et al. (2019). Both inferences, drawn from distinct sets of loci, recovered the focal lineage in a cluster further comprising the three aforementioned genera, and hence independently supporting the establishment of the new genus. In fact, the newly introduced genus, whose representatives were treated as species of *Lobaria* until now, are not closely related to either *Lobaria* or *Ricasolia*, although morphologically it is most similar to the latter (Yoshimura 1998). Since no generic or infrageneric name is available for this clade, we introduce the genus *Emmanuelia*, currently comprising the following twelve species: *E. americana*, *E. conformis*, *E. cuprea*, *E. elaeodes*, *E. erosa*, *E. excisa*, *E. lobulifera*, *E. ornata*, *E. patinifera*, *E. pseudolivacea*, *E. ravenelii* and *E. tenuis*. *Emmanuelia ravenelii* is designated as the nomenclatural type for the genus, since this is probably the best-documented species of the lineage and its identification is straightforward.

The low backbone support for phylogenetic relationships within *Emmanuelia* may be due to a recent rapid radiation, an evolutionary scenario recently highlighted within the *Lobarioideae* (Lücking et al. 2017b; Simon et al. 2018). Based on our time-calibrated phylogeny, this clade emerged approximately 10 million years ago in the late Miocene, making this one of the younger genera within the *Lobarioideae* (Widhelm et al. 2019). However, other related genera such as *Lobariella*, *Lobarina*,

Ricasolia and *Yoshimuriella* have similar crown ages, whereas *Dendriscosticta* and particularly *Lobaria* s.str. appear to be older. The fairly restricted geographic distribution of *Emmanuelia*, as compared to other more widespread related genera, tends to support the scenario of a recent diversification. Notably, the crown divergence time for *Emmanuelia* coincides with the onset of the uplift of the northern Andes (Hoorn et al. 2010). The latter may explain the rather recent diversification of genera such as *Lobariella* (Moncada et al. 2013), but most of the *Emmanuelia* species occur in the Atlantic Forest of south-eastern Brazil, in a geologically much older formation (Peucker-Ehrenbrink & Miller 2007; Brotzu et al. 2007; Colombo & Joly 2010). Possibly the recent diversification of *Emmanuelia* largely in the Atlantic Forest, with subsequent expansion northwards, is related to paleoclimatic events, as apparent from other groups of organisms in this biome with similarly recent diversification times (e.g., Fouquet et al. 2012; Batalha-Filho et al. 2013; Machado et al. 2018).

Low taxonomic resolution possibly resulting from recent diversification is particularly evident in the *E. elaeodes* aggregate, where morphological identifications do not necessarily correspond to phylogenetic topology (with the exception of *E. ravenelii*). Two possible reasons for this may be offered: (1) the ITS and mtSSU markers

may not be sufficiently informative to disentangle species within this complex, or (2) this complex may represent a single species with morphological variation. In particular, *E. tenuis* may represent the phyllidiate counterpart of *E. elaeodes*. Further studies are needed to resolve the taxonomy of this complex.

Taxonomy

Emmanuelia Ant. Simon, Lücking & Goffinet, gen. nov.

Mycobank MB 834643

Diagnosis: A lobarioid genus lacking cyphellae, pseudocyphellae and maculae, with a short, \pm uniform lower tomentum (no veins), primarily associated with a green alga, sometimes with a dendriscocauloid cyanomorph, with gyrophoric acid (major) and 4-O-methylgyrophoric acid (congyrophoric acid; minor or absent) as secondary compounds. Morphologically and chemically similar to the genus *Ricasolia*, but differing in the apothecia with overarching margin and separation of the parathecium and amphithecium, consistently narrower and longer, acicular ascospores, and a subtropical to tropical distribution. Molecularly, the new genus is characterized by a short, unique rDNA sequence motif within the highly conserved 5.8S region in the ITS. The section defining *Emmanuelia* is as follows (deviations underlined):

5-CGAATCATCGAATCTTTGAACGCACATTGCGC-CCCYGGYAC-3.

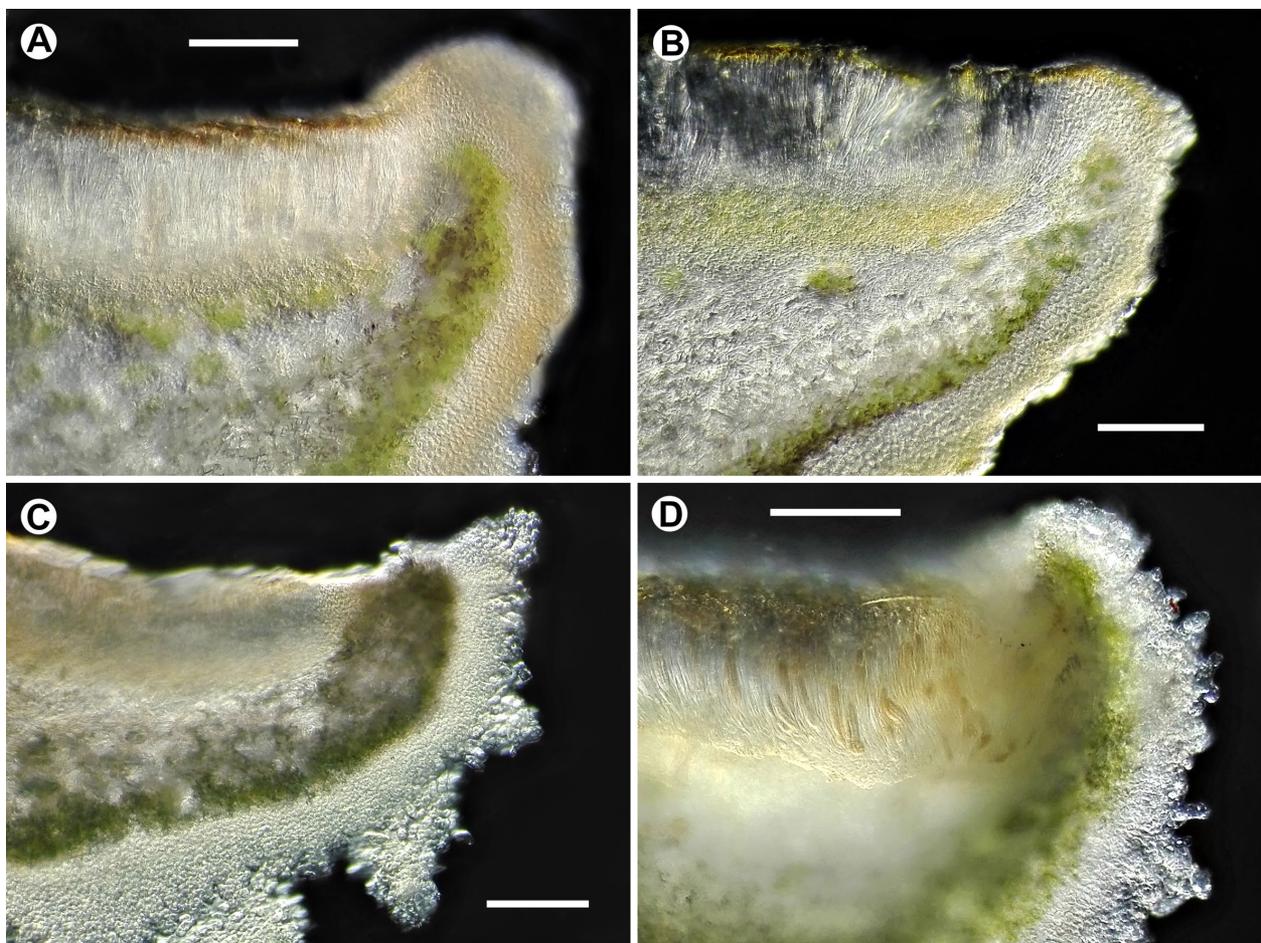


Figure 3. Apothecial sections in *Emmanuelia* and *Ricasolia*. A–B – *R. quercizans* (A, Wetmore 83137) and *R. virens* (B, Sipman 1742), showing the parathecium apically connected with the amphithecium; C–D – *E. ravenelii* (Harris 14938) and *E. elaeodes* (Lücking 37544a), showing the parathecium apically separated from the amphithecium by the photobiont layer. Scale = 100 μ m.

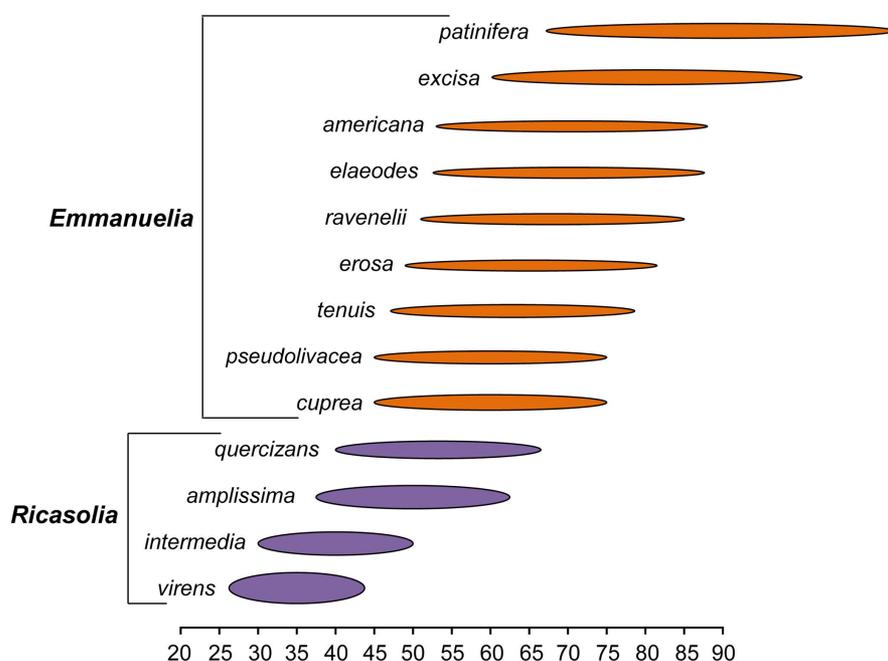


Figure 4. Comparison of ascospore dimensions in *Ricasolia* and *Emmanuelia*. Each ellipse indicates mean ascospore length and width; the ellipses are positioned according to their mean length.

Generic type: *Emmanuelia ravenelii* (Tuck.) Ant. Simon & Goffinet

Etymology. The new taxon is named in honor of Prof. Emmanuël Sérusiaux, for his extensive contributions to advancing our understanding of the diversification of the *Peltigerales*.

Comments. Morphologically, *Emmanuelia* can be easily differentiated from *Lobaria* s.str. by the tomentum on the lower surface and the shape of the ascospores (Yoshimura 1998; Moncada et al. 2013). However, the newly introduced genus is quite similar to *Ricasolia*. In particular, like some species of *Ricasolia*, at least one species of *Emmanuelia*, *E. ornata* (previously often identified with the name *Lobaria patinifera*), produces dendriscoauloid cyanomorphs emerging from the green-algal thallus (e.g., Jordan 1972; Tønsberg et al. 2016; Fig. 6C–D). The two genera differ in their geographical distribution and ecology: *Emmanuelia* is a subtropical to tropical taxon found from southeastern North America to southern South America, whereas *Ricasolia* appears to be a strictly temperate, Northern Hemisphere taxon (Cornejo et al. 2017); the two genera are somewhat sympatric in the southeastern United States, but *Emmanuelia* replaces *Ricasolia* in coastal areas (Jordan 1973).

Morphologically, *Emmanuelia* differs from *Ricasolia* by its apothecia, rimmed by overarching and often crenulate to lobulate margins with a rough surface, whereas in *Ricasolia* the margins are only slightly prominent, more or less entire, and with a smooth surface, an observation also noted by Yoshimura (1998) when comparing tropical species of his '*Lobaria quercizans* group' to *Ricasolia quercizans* s.str. Anatomically, in *Emmanuelia* the parathecium (proper excipulum) appears to be apically separated from the amphithecium (formed by the thallus

cortex), by the photobiont layer reaching up to the apex, and also different in structure (prosoplectenchymatous vs. paraplectenchymatous), a characteristic referred to as 'apothecium type II' (Yoshimura 1971; Yoshimura & Osorio 1975). In *Ricasolia* the parathecium and amphithecium are apically connected, due to the photobiont layer stopping short distinctly below the apex, and at least the upper part of the parathecium is paraplectenchymatous. A further difference is found in the ascospores, with those of *Emmanuelia* generally acicular and arranged in a bundle and those of *Ricasolia* fusiform and irregularly arranged to uniseriate.

Below we provide brief diagnostic descriptions and comments for ten of the 12 species included in the new genus, and more detailed accounts for the type species, *E. ravenelii*, and the reinstated eastern North American *E. lobulifera*.

Emmanuelia americana (Vain.) Lücking, Moncada & Gumboski, comb. nov. (Fig. 5A)

Mycobank MB 834644

Basionym: *Lobaria americana* Vain., Acta Soc. Fauna Fl. Fenn. 7(1): 195. 1890.

Type: Brazil, Minas Gerais: Serra do Caraca; 1400 m, 1885, Vainio 1187 (TUR-V10666 – lectotype!, here selected; MBT391290; M-M0207349 – isolectotype!).

Diagnostic description. Primary photobiont a trebouxoid alga. Thallus medium-sized to large, rather loosely adnate, composed of irregularly arranged lobes. Lobes leathery, rather broad, up to 12 mm wide, sinuose with ±rounded apices. Upper surface ±even but often with abundant pycnidial warts, glabrous. Lower surface thinly tomentose except for bare marginal zone, tomentum brown. Apothecia scattered, laminal, to 7 mm in diam.,

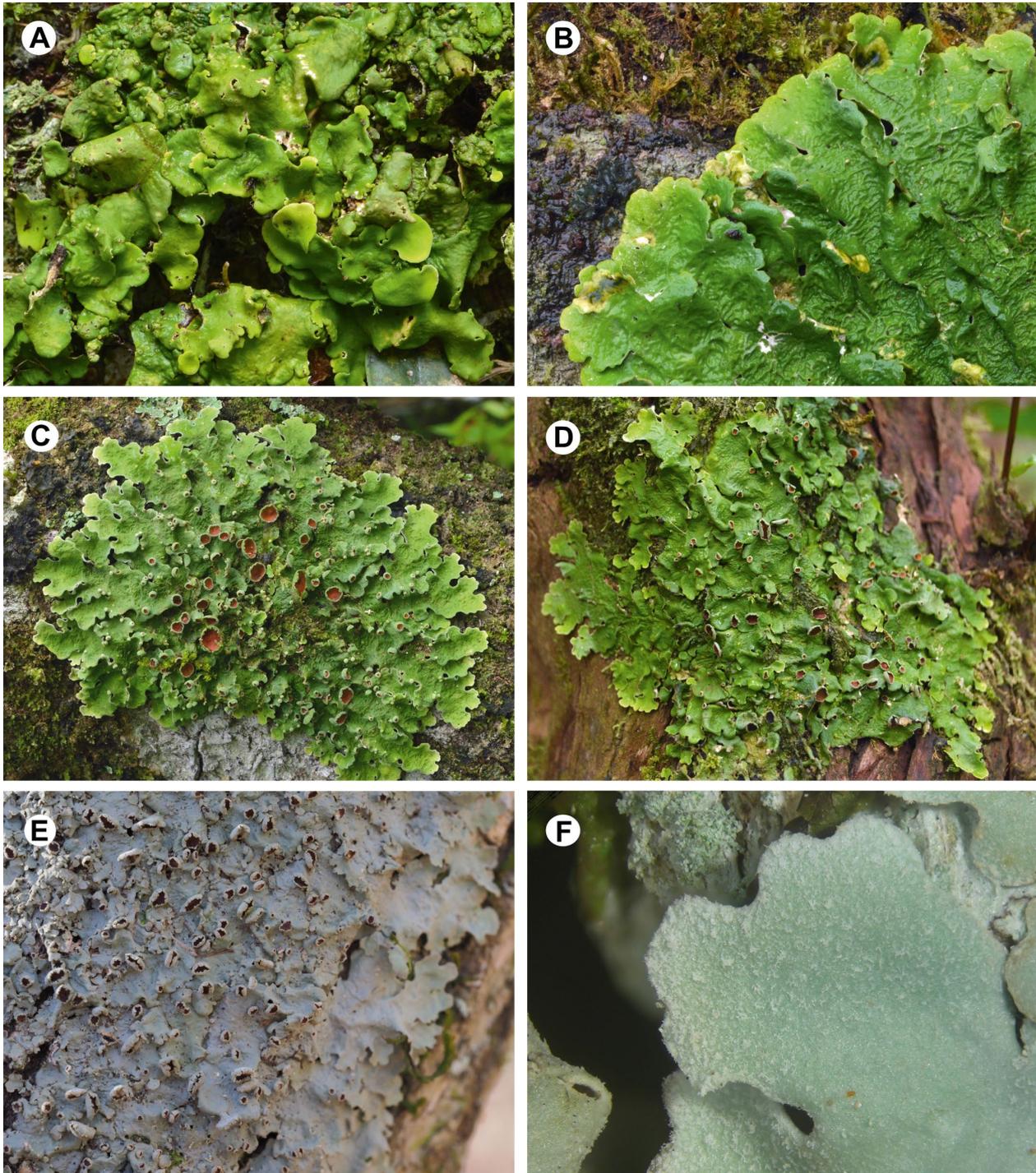


Figure 5. Habit of *Emmanuelia* species. A – *E. americana* (Lücking 40112), showing upper side with pycnidial warts; B – *E. erosa* (Cáceres 25148), showing upper side with distinct scrobiculate surface; C–D – *E. elaeodes* (C, Lücking 40082; D, Lücking 37546), showing upper side with apothecia; E–F – *E. ravenelii* (Hollinger 2332, CONN), showing upper side with numerous apothecia (E) and close-up of lobe margins with pruinose surface (F). Photographs E & F: courtesy of Jason Hollinger.

margin strongly prominent, lobulate. Ascospores acicular, straight to slightly curved, 1(–3)-septate, $60\text{--}80 \times 2.5\text{--}3 \mu\text{m}$, ~20–30 times as long as broad.

Secondary chemistry. Gyrophoric acid (major).

Comments. This species is intermediate between *Emmanuelia patinifera* and *E. elaeodes* in thallus and lobe size and in the development of a lobulate apothecial margin, but has generally a thicker thallus with a leathery appearance. While molecular data and morphology clearly

separate *E. elaeodes* from *E. patinifera*, *E. americana* is phylogenetically close to *E. elaeodes*.

Specimens examined. BRAZIL. Santa Catarina: São Francisco do Sul, Parque Estadual Acarai; $26^{\circ}16'S$, $48^{\circ}32'W$, sea level; rather well preserved coastal Restinga forest; 8 October 2015, Lücking 40112 (B, JOI). São Paulo: Guapiara, Serra Paranapiacaba, Fazenda Intervales, just W of ‘Sede de Pesquisas’; $24^{\circ}16'N$, $48^{\circ}25'W$, 800 m; hilly, humid forest along stream; 23 July 1991, D. M. Vital & W. R. Buck 20429 (B).

Molecular data. Yes.

Emmanuelia conformis (Nyl.) Lücking, Moncada & Ant. Simon, comb. nov.

Mycobank MB 834645

Basionym: *Lobaria conformis* Vain., Dansk Bot. Ark. 4(11): 16. 1926.

Types: Mexico, Veracruz: Totutla, Mirador, Aguas Santos; 1841, Liebmann 7545 (TUR-V10658 – lectotype!, here selected, MBT391291). [Mexico] Veracruz: Totutla; 1841, Liebmann 7546 (TUR-V10659 – paratype!). Pico de Orizaba; 1841, Liebmann 7564 (TUR-V10660!). Huatusco; 1841, Liebmann 7565 (TUR-V10663 – paratype!), Liebmann 7570 (TUR-V10664 – paratype!). Mirador; 1842, Liebmann 7581 (TUR-V10661, TUR-V10662 – paratypes!).

Diagnostic description. Primary photobiont a trebouxoid alga. Thallus small, closely adnate, composed of \pm radiating lobes. Lobes narrow, up to 3 mm wide, sinuose with undulate margins and rounded apices. Upper surface \pm even, glabrous. Lower surface thinly tomentose except for narrow, bare marginal zone, tomentum greyish brown. Apothecia frequent, laminal, to 3 mm in diam., margin prominent, shallowly crenulate. Ascospores acicular, straight to slightly curved or sigmoid, 3–5-septate, $70\text{--}80 \times 2\text{--}3 \mu\text{m}$, $\sim 25\text{--}35$ times as long as broad.

Secondary chemistry. Gyrophoric acid (major).

Comments. This material was first considered conspecific with *Emmanuelia elaeodes* (see comments below) but differs in the overall much smaller size and in the 3–5-septate ascospores, as well as in its distribution. Yoshimura (1998) considered *Lobaria conformis* a synonym of *L. patinifera*, with the latter name in his treatment being misapplied to what is here recognized as *E. ornata*. However, *E. conformis* differs from both *E. ornata* and *E. patinifera* (see key below). Notably, several studies had reported *L. conformis* as a separate species prior to Yoshimura's (1998) treatment (e.g., Osorio & Fleig 1987; Sipman 1993).

Molecular data. No.

Emmanuelia cuprea (Müll. Arg.) Lücking, Moncada & Ant. Simon, comb. nov.

Mycobank MB 834646

Basionym: *Ricasolia cuprea* Müll. Arg., Revue Mycol. 10(38): 55. 1888.

Types: Paraguay, 'Cordillère de Péribébuy' [sic]; Jul 1879, Balansa 4211 (G-G00292338 – lectotype!; G-G00292342 – isolectotype!). [Brazil] Rio Grande do Sul: without locality, Blumenau s.n. (G-G00292344 – paratype!).

= *Lobaria cuprea* (Müll. Arg.) Zahlbr., Cat. Lich. Univers. 3: 299. 1925.

Diagnostic description. Primary photobiont a trebouxoid alga. Thallus medium-sized, rather closely adnate, composed of \pm radiating lobes. Lobes intermediate, up to 10 mm wide, sinuose with rounded apices. Upper surface \pm even, glabrous. Lower surface thinly tomentose except for bare marginal zone, becoming purplish red in

the herbarium, tomentum greyish brown. Apothecia scattered, laminal, to 8 mm in diam., margin strongly prominent, shallowly to deeply crenulate. Ascospores acicular, straight to slightly curved or sigmoid, 1-septate, $55\text{--}65 \times 3.5\text{--}4 \mu\text{m}$, ~ 15 times as long as broad.

Secondary chemistry. Gyrophoric acid (major) and unknown purple pigment appearing post-mortem after rewetting (Yoshimura & Osorio 1975).

Comments. This taxon is characterized by the purplish red color of the underside in rewetted herbarium specimens (Yoshimura & Osorio 1975; Osorio & Fleig 1987); this corresponds to a specific pigment detectable by TLC (Yoshimura & Osorio 1975). A similar effect has been reported for, e.g., *Cora rubrosanguinea* from Ecuador (Lücking et al. 2017a).

Molecular data. No.

Emmanuelia elaeodes (Malme) Lücking, Spielmann & S. M. Martins comb. nov. (Fig. 5C–D)

Mycobank MB834647

Basionym: *Lobaria elaeodes* Malme, Ark. Bot. 26A(14): 4. 1935.

Type: Brazil, Mato Grosso: Serra da Chapada, Buriti; 25 Jun 1894, Malme 2492b (S-L1564 – holotype!).

Diagnostic description. Primary photobiont a trebouxoid alga. Thallus medium-sized, rather closely adnate, composed of \pm radiating lobes. Lobes intermediate, up to 7 mm wide, sinuose with rounded to truncate apices. Upper surface \pm even, glabrous except for sometimes scattered tiny hairs near the apices. Lower surface thinly tomentose except for narrow, bare, whitish marginal zone, tomentum greyish brown. Apothecia frequent, laminal, to 3 mm in diam., margin strongly prominent, shallowly to deeply crenulate. Ascospores acicular, straight to slightly curved or sigmoid, 1(–3)-septate, $60\text{--}80 \times 2.5\text{--}3 \mu\text{m}$, $\sim 20\text{--}30$ times as long as broad.

Secondary chemistry. Gyrophoric acid (major), 4-O-methylgyrophoric (congyrophoric) acid (minor).

Comments. We first named the Brazilian material *Ricasolia intermedia*, a species described from Mexico. The type material of *Lobaria elaeodes*, *Ricasolia intermedia*, and *L. conformis*, also described from Mexico, all agree in thallus morphology and lobe disposition. However, after discovering the differences in ascospore size and shape between *Emmanuelia* and *Ricasolia*, we noticed that the ascospores of *R. intermedia*, not given in the protologue, were described as rather short and broad by Stizenberger (1895), namely $\sim 35\text{--}45 \times 10 \mu\text{m}$, $\sim 3.5\text{--}4.5$ times as long as broad. On the type material, also rather broad ascospores are depicted, without measurements but ~ 7 times as long as broad. In contrast, the ascospores of the types of *L. elaeodes* and *L. conformis* fit those of *Emmanuelia*. Therefore we consider *R. intermedia* a genuine member of that genus, whereas the Brazilian material represents the genus *Emmanuelia* and must bear

the epithet *elaeodes*. The Mexican *L. conformis* is also considered a species of *Emmanuelia* but it differs from *E. elaeodes* by the smaller thallus with narrower lobes and the multiseptate ascospores.

Specimens examined. BRAZIL. Rio Grande do Sul: Caraá, Caraá Environmental Protection Area; 29°42'S, 50°17'W, 410 m; well-preserved Atlantic Forest fragment; 21 September 2014, Lücking 37511, 37545, 37544a, 37546 (B, HAS). Santa Catarina: São Francisco do Sul, Parque Estadual Acarai; 26°16'S, 48°32'W, sea level; rather well preserved coastal Restinga forest; 8 October 2015, Lücking 40082, 40112 (B, JOI).

Molecular data. Yes.

Emmanuelia erosa (Eschw.) Lücking, M. Cáceres & Ant. Simon, comb. nov. (Fig. 5B)

Mycobank MB 834648

Basionym: *Parmelia erosa* Eschw. in Martius, Fl. Bras. Enum. Pl. 1(1): 211. 1833.

Type: Brazil, Minas Gerais: Without locality ('serro frio'); Martius s.n. (M-M0024300 – holotype!).

≡ *Ricasolia erosa* (Eschw.) Nyl., Syn. Meth. Lich. 1(2): 371. 1860.

≡ *Lobaria erosa* (Eschw.) Trevis., Lichenoth. Veneta 1–2: 75. 1869.

≡ *Sticta erosa* (Eschw.) Tuck., Syn. N. Amer. Lich. 1: 93. 1882.

≡ *Lobaria quercizans* var. *erosa* (Eschw.) Vain., Acta Soc. Fauna Fl. Fenn. 7(1): 196. 1890.

Diagnostic description. Primary photobiont a treboux-ioid alga. Thallus small to medium-sized, closely adnate, composed of irregular to ±radiating lobes. Lobes narrow, up to 5 mm wide, with truncate apices. Upper surface distinctly scrobiculate, glabrous. Lower surface thinly tomentose except for bare marginal zone, tomentum greyish brown. Apothecia frequent, laminal, to 5 mm in diam., margin strongly prominent, lobulate but lobules caducous. Ascospores acicular, straight to slightly curved or sigmoid, 1-septate, 60–70 × 2.5–3 µm, ~20–25 times as long as broad.

Secondary chemistry. Gyrophoric acid (major).

Comments. This is a rather characteristic species, which in the past had been synonymized with *Emmanuelia* (as *Lobaria*) *ravenelii* and even *Ricasolia quercizans* (e.g., Stizenberger 1895), but its rather narrow, scrobiculate lobes are distinctive and its separation is supported by molecular data.

Specimens examined. BRAZIL. Rio de Janeiro: Itatiaia National Park, Agulhas Negras road, km 8 on road to Agulhas Negras, 32 km NW of Itatiaia, roadside; 22° 21'S, 44° 44'W, 2150 m; Atlantic Rain Forest, small roadside forest fragment near *Araucaria* stand, on bark; 6 May 2015, M. E. S. Cáceres et al. 25148 (B, ISE). São Paulo: Praia do Lázaro bei Ubatuba; 2 m; in einem hellen und trockenen Stranddünenwald (Restinga); 29 September 1979, K. Kalb (B); distributed in *Lichenes Neotropici*, no. 237, as *Lobaria ravenelii*.

Molecular data. Yes.

Emmanuelia excisa (Müll. Arg.) Lücking, Moncada & Ant. Simon, comb. nov.

Mycobank MB 834649

Basionym: *Sticta excisa* Müll. Arg., Flora 74: 375. 1891.

Type: Colombia, unknown locality; on rotten trunk; Blagborne s.n. (M-M0207328 – lectotype!, here selected, MBT391292; G-G00294960 – isolectotype!).

≡ *Ricasolia excisa* (Müll. Arg.) Stizenb., Flora 81: 112. 1895.

≡ *Lobaria excisa* (Müll. Arg.) Zahlbr., Catal. Lich. Univers. 3: 301. 1925.

Diagnostic description. Primary photobiont a treboux-ioid alga. Thallus medium-sized to large, closely adnate, composed of radiating lobes. Lobes intermediate, up to 10 mm wide, sinuose with undulate margins and rounded to crenulate apices. Upper surface ±even to somewhat canaliculate, glabrous. Lower surface dense and very regularly tomentose except for narrow, bare, pale marginal zone, tomentum dark brown. Apothecia frequent, laminal, to 5 mm in diam., margin strongly prominent, distinctly lobulate. Ascospores acicular, straight to slightly curved, 1–3-septate, 70–90 × 3.5–4 µm, ~20–25 times as long as broad.

Secondary chemistry. Gyrophoric acid (major).

Comments. Müller (1891) described *Sticta excisa* from Colombia and Jamaica. There are three syntypes in G (Colombia, Jamaica) and M (Colombia). The material from Jamaica does not bear apothecia, so its identity cannot be ascertained. Therefore the well-developed specimen from Colombia in M was selected as lectotype. *Emmanuelia excisa* is somewhat intermediate between *E. patinifera* and *E. elaeodes* but it differs from the first in the narrower, radiating, adnate lobes and smaller, horizontal apothecia, and from the second in the more robust thallus and distinctly lobulate apothecial margins. The ascospores of *E. excisa* are the among the broadest thus far known in the genus, but still narrower than those of *Ricasolia quercizans* (Fig. 4).

Specimen examined. COLOMBIA. Casanare: Chámeza, Vda. Mundo Viejo, finca El Triunfo; 5°11'39"N, 72°54'06"W, 1450 m; on bark; 24–31 January 2012, L. Vargas & J. Herrera 551 (UDBC-C-0004830).

Molecular data. No.

Emmanuelia lobulifera (B. Moore) Ant. Simon & Goffinet, comb. nov. (Fig. 6A–B)

Mycobank MB 834650

Basionym: *Lobaria lobulifera* B. Moore, The Bryologist, 72(3): 404. 1969.

Types: USA, Florida, Citrus County: Yulee Sugar Mill, Moore 1042 (DUKE – holotype!; US – isotype!). Columbia County: Junction of Florida Highway 6 and US Highway 441, Hale 21777 (US – paratype!); O'Leno State Park, Hale 16436 (US – paratype!). Duval County: Jacksonville, Calkins 38 (US – paratype!). Flagler County: Near Bunell, Moore 2440 (DUKE – paratype!). Orange County: Rock Springs, Moore 3772a (DUKE – paratype!).

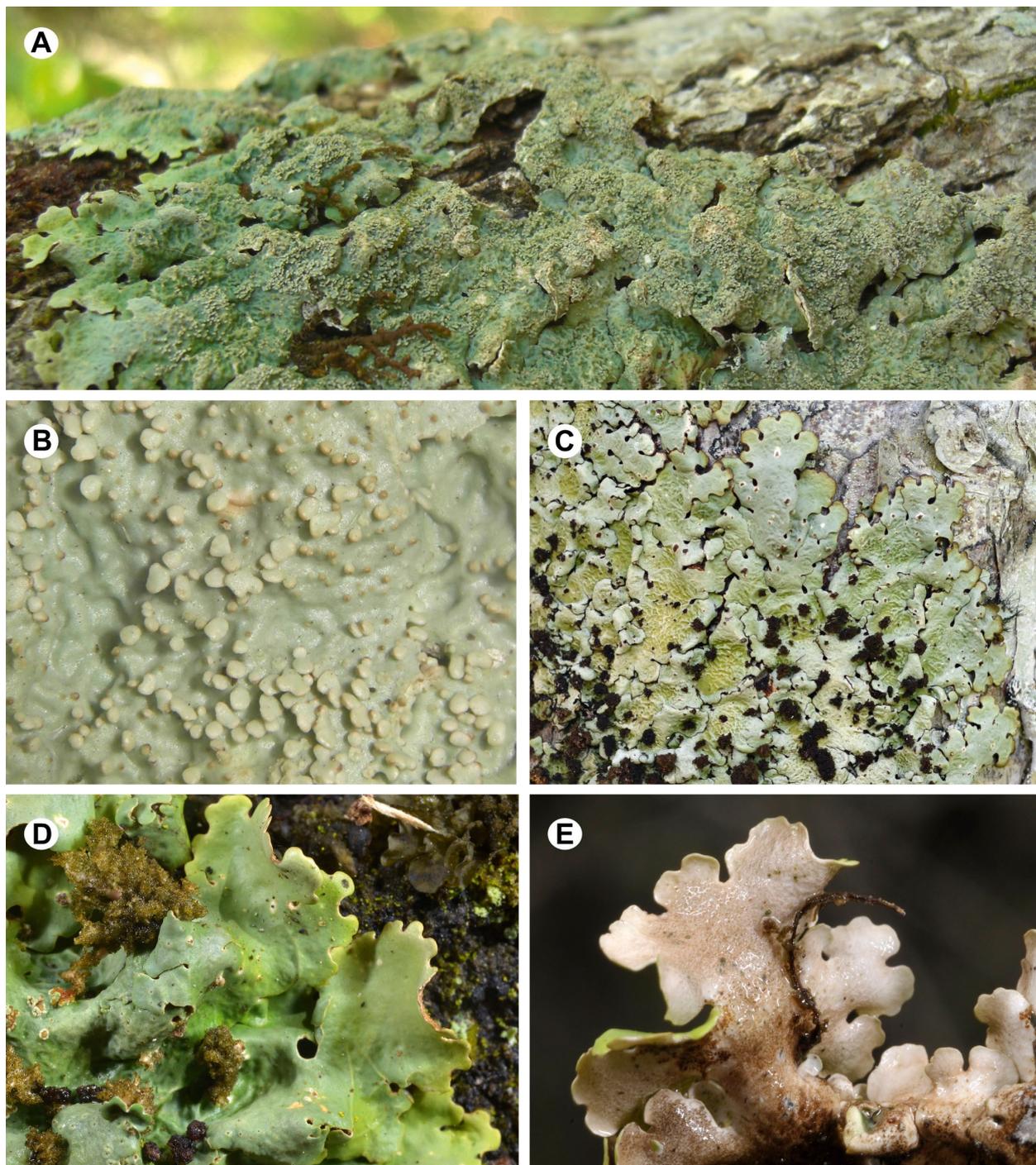


Figure 6. Habit of *Emmanuelia* species. A–B – *E. lobulifera* (Hollinger 2542), showing upper side with sparsely branched phyllidia (A) and phyllidia enlarged (B); C–E – *E. ornata*, showing upper side with dendriscoauloid cephalodia (C, Moncada 8401, CDS 55273), cephalodia enlarged (D, Bungartz 10972, CDS 55363), and lower side (E, Bungartz 10244, CDS 47663). Photographs A, B: courtesy of Jason Hollinger.

Description. Primary photobiont a trebouxioid alga. Thallus irregular in outline, small to medium-sized, to 8 cm diam., composed of radiating, stiff, repeatedly branched and spreading lobes. Lobes adjacent to imbricate and overlapping, from 1 mm wide at branching point and to 5 mm wide above, with truncate to spatulate apices, adnate, with free, plane margins; margins entire, occasionally with small simple lobules inward. Upper surface smooth, glabrous, light greenish or rarely brownish grey and light brownish towards margin when dry, greenish when wet, matte; margin lacking pruina. Phyllidia mostly laminal, somewhat obliquely oriented, squamiform, almost

orbicular to palmate, mostly unbranched to sparsely branched, either at base or along margin bearing one or more lobules, or dichotomously branched, typically ~0.5 mm in diam., to 1 mm long. Medulla rather compact, white, KC+ pink. Cephalodia (with *Nostoc*) internal, globose, to 0.2 mm in diameter. Lower surface smooth at margin, rugose, verrucose inward, thinly tomentose, with hairs in short fascicles, light brown to cream-colored. Rhizines simple, abundant to scattered, to 0.8 mm long, whitish, darkening inward. Apothecia not observed. Upper cortex paraplectenchymatous, 20–30 µm thick, homogeneous, consisting of 4–6 cell layers. Photobiont

layer 15–30 µm thick, its cells ~6 µm diam. Medulla 60–100(120) µm thick. Lower cortex paraplectenchymatous, 15–20 µm thick, with 3 cell layers; surface papillose to microtomentose in section in between short fascicles.

Secondary chemistry. Gyrophoric acid (major), 4-O-methylgyrophoric acid (minor).

Ecology and distribution. On hardwood trees on the coastal plain of the southeastern United States.

Comments. Our study revealed that *Lobaria lobulifera* (Moore 1969), previously synonymized under *L. tenuis*, is a distinct species, here resurrected as *E. lobulifera*. The shared presence of phyllidia led Yoshimura (1971) and Jordan (1973) to synonymize the two taxa, but both the position of the phyllidia (largely laminal vs. marginal) and their shape (squamiform vs. elongate) differ between *E. lobulifera* and *E. tenuis*, and their distinction is supported by phylogenetic data. The different distribution of the two taxa provides another argument, with *E. tenuis* mostly known from Brazil (e.g., Lücking 37544b, 40067), including the type, and *E. lobulifera* from the southeastern United States (e.g., Kaminski LK450, Lendemer 21578, 41467, and Rosentreter 19739), with its type collected in Florida (Moore 1969).

Specimens examined. USA. Alabama, Covington Co., Conecuh National Forest, Solon Dixon Forestry Education Center, Cave Road, 31.1864°, –86.6972°, extensive limestone outcroppings, mesic hardwoods, on trunk of *Fagus*, 2007 April 14, W. R. Buck 51821 (NY #919534); Florida, Levy Co., N end of Gulf Hammock, along St. Rd. 24, 7.5 mi SW of US 19/98 at Otter Creek, 29°16'N, 82°52'W, hardwood–*Taxodium* swamp, on *Fraxinus*, 1995 December 31, R. C. Harris 37160 (NY); Suwannee Co., Peacock Springs State Recreation Area, off 180th Street 2.2 mi E of FL 51 at Luraville, 30°07'N, 83°08'W, upland hardwood forest around limestone springs, on old fallen oak, 1996 December 2, R. C. Harris 39371 (NY); Georgia, Appling Co. Moody Forest Natural Area, 0–0.5 mi E of head of River Trail on Miller Landing Rd., 0.75 mi N of jct w/ E River Road, 31.9167, –82.2681, oak scrub with pine and occasional larger hardwoods, on *Liquidambar*, 2009 December 17, J. C. Lendemer 21063 (NY #1151402); Effingham Co., Craig Barrow farm, 32.3526°, –81.4804°, north-aspect sandhill bluff, on bark, 2012 March 4, M. F. Hodges 8274 (NY #2057448); Emanuel Co., Ochoopee Dunes Natural Area, McLeod Bridge tract, 0.5 mi W of intersection of McLeod Bridge Road and Old McLeod Bridge Road, E shore of the Little Ochoopee River, 32.6028°, –82.4292°, oak scrub on white sand dunes grading into mixed hardwood forest, on *Quercus*, 2009 December 19, J. C. Lendemer 21288 (NY #1150245); Tattnall Co., Big Hammock Natural Area, blue and yellow trails, ~1 mi E of jct of CR 441 & GA 121/144/169, 31.8576°, –82.0589°, sandhill community with oak scrub and mixed hardwoods, on *Quercus*, 2009 December 20, J. C. Lendemer 21434 (NY #1150291); Wayne Co., Sansavilla Wildlife Management Area, Boat Launch below Alex Creek, SW shore of Altamaha River, 31.5111°, –81.6667°, steep mesic riverine bluff mixed hardwood forest (*Ilex*, *Carya*, *Quercus*, *Magnolia*, *Nyssa*) with NE aspect, on *Carya* base, 2009 December 21, J. C. Lendemer 21575 (NY #1150405); South Carolina, Berkeley Co., Francis Marion National Forest, Guilliard Lake Scenic Area, E of Gravel Run, W of FS 150-G, 0.5 mi S of terminus at Guilliard Lake and 0.3 mi SW of jct w/ FS 190, 33.2814°, –79.6244°, 20, upland mixed hardwood (*Acer*, *Quer-*

cus, *Liquidambar*, *Ilex opaca*, *I. laevigata*, *Myrica*) and *Pinus* forest, on *Quercus*, 2013 December 6, J. C. Lendemer 41467 (NY #2327058).

Molecular data. Yes.

Emmanuelia ornata (Malme) Lücking, Moncada & Bungartz, comb. nov. (Fig. 6C–E)

MycoBank MB 834652

Basionym: *Lobaria ornata* Malme, Ark. Bot. 26A (14): 5a. 1935.

Type: Brazil, Minas Gerais: São João del Rei; 1 Sep 1892, Malme 303 (S-L1557)

Diagnostic description. Primary photobiont a trebouxiioid alga. Thallus medium-sized, closely adnate, composed of radiating lobes. Lobes narrow, up to 5 mm wide, with rounded to truncate apices. Upper surface ± even to shallowly scrobiculate towards center, glabrous. Lower surface thinly tomentose except for a bare, whitish marginal zone, tomentum brown. Apothecia not observed.

Secondary chemistry. Gyrophoric acid (major), 4-O-methylgyrophoric (congyrophoric) acid (minor).

Comments. This species is here reported for the first time from the United States and the Galapagos Islands. North American material was previously considered a form of *Lobaria ravenelii* with erumpent cephalodia (Jordan 1973). In tropical America this taxon was mostly named *L. patinifera*, but the type of the latter is entirely different from the material with narrow, adnate lobes and cephalodia to which this name has been applied (see below). The dendriscoauloid cephalodia are reminiscent of those of *Ricasolia* species, and since apothecia are apparently absent in this species, it cannot be readily assigned to *Emmanuelia* without molecular data.

Molecular data. Yes.

Emmanuelia patinifera (Taylor) Lücking, M. Cáceres & Ant. Simon, comb. nov. (Fig. 7A)

MycoBank MB 834653

Basionym: *Parmelia patinifera* Taylor, London J. Bot. 6: 172. 1847.

Type: Brazil, Rio de Janeiro: Serra dos Órgãos; Gardner et al. 1002 (G-G00291728 – isotype!).

- ≡ *Ricasolia patinifera* (Taylor) Müll. Arg., Flora 71: 24. 1888.
- ≡ *Sticta patinifera* (Taylor) Müll. Arg., Flora 74: 111. 1891.
- ≡ *Lobaria patinifera* (Taylor) Hue, Nouv. Arch. Mus. Hist. Nat., Paris, 4, Sér. 3: 29. 1901.
- = *Sticta casarettiana* De Not., Mém. R. Accad. Sci. Torino, Ser. 2 12: 158. 1851.
- = *Squamaria casarettiana* (De Not.) A. Massal., Atti Inst. Veneto Sci. lett., ed Arti, Sér. 3, 5: 250. 1860.
- = *Ricasolia casarettiana* (De Not.) Nyl., Acta Soc. Sci. Fenn. 7(2): 438. 1863.
- = *Lobaria casarettiana* (De Not.) Trevis., Lichenoth. Veneta: no. 75. 1869.
- = *Ricasolia erosa* var. *casarettiana* (De Not.) Nyl., Flora 52: 314. 1869.

= *Ricasolia quercizans* var. *casarettiana* (De Not.) Stizenb., Flora 81: 112. 1895.

= *Lobaria quercizans* f. *casarettiana* (De Not.) Zahlbr., Cat. Lich. Univers. 10: 272. 1939.

Type: Brazil, Rio de Janeiro: Serra dos Órgãos; Casaretto 851 (H-NYL 33432 – H-H9506039 – isotype!).

= *Ricasolia erosa* var. *laevis* Müll. Arg., Flora, Regensburg 63: 264. 1880.

Type: Brazil, Rio de Janeiro: Without locality; 1878, Glaziou 2789 (G-G00294980 – lectotype!, here selected, MBT391293).

= *Lobaria quercizans* f. *aequalis* Vain., Acta Soc. Fauna Fl. Fenn. 7(1): 196. 1890.

Type: Brazil, Minas Gerais: Sitio; 1000 m; 1885, Vainio 954 (TUR-V10651 – holotype!).

Diagnostic description. Primary photobiont a trebouxioid alga. Thallus large, loosely adnate, composed of irregularly arranged to somewhat radiating lobes. Lobes broad, up to 20 mm wide, with rounded to truncate apices. Upper surface uneven, glabrous. Lower surface thinly tomentose except for a broad, bare, whitish marginal zone, tomentum greyish brown. Apothecia frequent, laminal, to 10 mm in diam., typically obliquely arranged (almost as in *Peltigera* species), margin strongly prominent, coarsely lobulate, the parathecium in section formed by peculiar, thick, palisadic hyphae that break up under pressure into separate ‘hairs’. Ascospores acicular, straight to slightly curved, 3-septate, $85\text{--}95 \times 3.5\text{--}4 \mu\text{m}$, ~20–25 times as long as broad.

Secondary chemistry. Gyrophoric acid (major).

Comments. The name *Lobaria patinifera* has been commonly misapplied to specimens with an adnate thallus, with narrow lobes and forming abundant, dendriscoauloid cephalodia. Revision of type material revealed that *Emmanuelia patinifera* is characterized by rather broad, loosely attached lobes, large, distinctly lobulate apothecia, and lack of external cephalodia. The type material of *Sticta casarettiana* and the other taxonomic synonyms listed here correspond well to this morphology. The ascospores of *E. patinifera* were described as 3–7-septate by some authors, but this was likely based on either wrongly identified specimens or misinterpretation of the septa of the very narrow ascospores. Typically the ascospores are 1-septate, occasionally 3-septate. *Emmanuelia patinifera* is a peculiar species, emerging from the earliest split in the genus in our ML tree: it has the largest thallus and most robust lobes, as well as the largest apothecia and ascospores in the genus; the apothecia are obliquely oriented, and the parathecium (proper exciple) is formed by peculiar, thick, palisadic hyphae. Magain et al. (2012) reported this species from Reunion (Mascarene archipelago), but the ITS sequence generated does not fall into *Emmanuelia* and their specimen may belong to *Lobariella*.

Specimens examined. BRAZIL. Minas Gerais: Itatiaia National Park, Agulhas Negras road, km 4 on road to Agulhas Negras, 34 km NW of Itatiaia, roadside; 22°22'S, 44°45'W, 1980 m; Atlantic Rain Forest, shady roadside forest margin, on bark; 6 May 2015; M. E. S. Cáceres et al. 25182 (B, ISE).

Molecular data. Yes.

Emmanuelia pseudolivacea (Zahlbr.) Lücking, Moncada & Ant. Simon, comb. nov.

MycoBank MB 834651

Basionym: *Lobaria pseudolivacea* Zahlbr., Cat. Lich. Univers. 3: 309. 1925.

Types: Brazil, Minas Gerais: Sitio; 1000 m; 1885, Vainio 376 (TUR-V10641 – lectotype!, here selected, MBT391295; TUR-V10642 – isolectotype!; M-M0207704 – isolectotype!). [Brazil] Minas Gerais: Sitio; 1000 m; 1885, Vainio 984 (TUR-V10643 – paratype!).

= *Ricasolia olivacea* Stizenb., Flora 81: 111. 1895 [nom. illeg., ICN Art. 53; non *Ricasolia olivacea* (Dufour) Bagl.].

= *Lobaria olivacea* Vain., Acta Soc. Fauna Fl. Fenn. 7(1): 197. 1890 [nom. illeg., ICN Art. 53; non *Lobaria olivacea* Hoffm.]; [nom. illeg., ICN Art. 52]

Diagnostic description. Primary photobiont a trebouxioid alga. Thallus medium-sized, closely adnate, composed of irregularly arranged lobes. Lobes narrow, up to 5 mm wide, often almost lacinate. Upper surface uneven, glabrous. Lower surface thinly tomentose except for narrow, bare marginal zone, tomentum greyish brown. Apothecia frequent, laminal, to 10 mm in diam., margin prominent, crenulate to lobulate. Ascospores acicular, straight to slightly curved, 1-septate, $55\text{--}65 \times 3\text{--}3.5 \mu\text{m}$, ~15–20 times as long as broad. No lichen substances.

Secondary chemistry. No substances detected by TLC.

Comments. This species is characterized by the rather narrow lobes combined with large apothecia, and the lack of secondary substances, an unusual feature in the genus, which is otherwise chemically uniform.

Molecular data. No.

Emmanuelia ravenelii (Tuck.) Ant. Simon & Goffinet, comb. nov. (Fig. 5E–F)

MycoBank MB 834654

Basionym: *Sticta ravenelii* Tuck., Amer. J. Sci. Arts, Ser. 2, 28: 203. 1859.

Type: USA, South Carolina: without locality; Ravenel s.n. (FH – lectotype!, here selected, MBT391294; US-US00432748 – isolectotype!). Cuba, without locality; Wright 66 p.p. (US-US00433359 p.p. – paratype!).

= *Ricasolia ravenelii* (Tuck.) Nyl., Acta Soc. Sci. Fenn. 7(2): 438. 1863.

= *Lobaria ravenelii* (Tuck.) Yoshim., J. Hattori Bot. Lab. 34: 320. 1971.

Description. Primary photobiont a trebouxioid alga. Thallus irregular in outline, small to medium to 11 cm diam., of radiating, stiff, repeatedly branched and spreading lobes. Lobes adjacent to imbricate and overlapping, to 5 mm wide between main dichotomies, with truncate to spatulate apices, adnate, with free, slightly broadly involute margins; margins entire, occasionally with small simple lobules inward. Upper surface smooth to scrobiculate, glabrous, light greenish or rarely brownish grey and light brownish toward margin when dry,

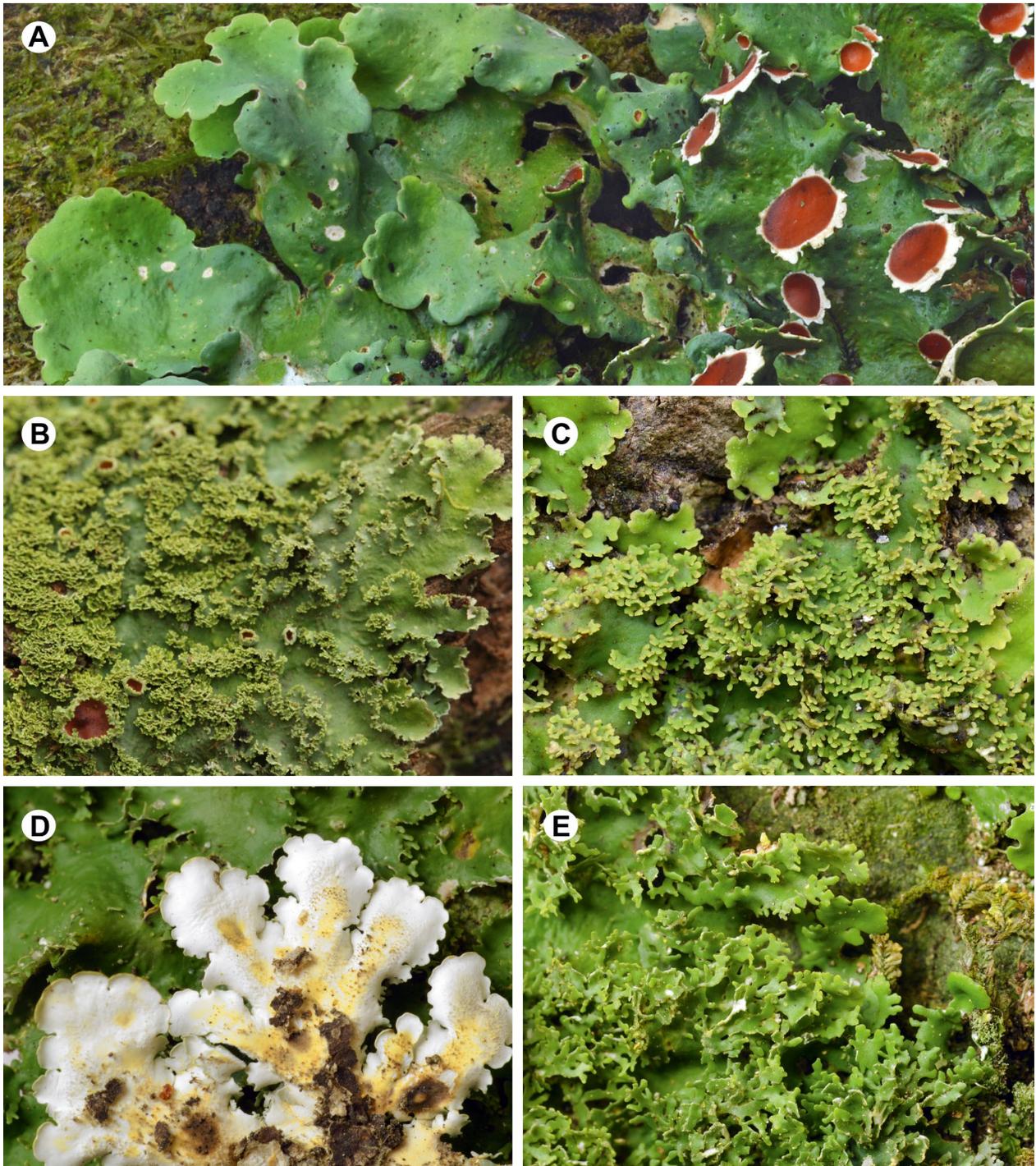


Figure 7. Habit of *Emmanuelia* species. A – *E. patinifera* (Cáceres 25182), showing upper side with lobulate apothecia; B–C – *E. tenuis* (B, Spielmann 11213, CGMS; C, Lücking 40067), showing upper side with apothecia and numerous phyllidia (B), and phyllidia enlarged (C); D–E – *E. aff. tenuis* (Lücking 39705), showing lower side (D) and upper side (E).

greenish when wet, matte; margin arachnoid-pruinose. Lobules generally absent, rarely marginal in older parts. Medulla rather compact, white, KC+ pink. Cephalodia (with *Nostoc*) internal, globose to flattened, to 0.4 mm wide, widely scattered. Lower surface smooth at margin, rugose, verrucose inward, thinly tomentose, with hairs in short fascicles, light brown-cream-colored. Rhizines simple, flaring, evenly scattered, to 1.5 mm long, brown, and darkening inward. Apothecia frequent but occasionally absent, laminal, scattered to abundant, to 5 mm in diam., margin shallowly to more rarely deeply crenulated,

marginal cortex pruinose, and ±rough. Upper cortex paraplectenchymatous, 20–30 µm thick, homogeneous, consisting of 4–6 cell layers. Photobiont layer 15–30 µm thick, its cells ~6 µm diam. Medulla 60–100(120) µm thick. Lower cortex paraplectenchymatous, 15–20 µm thick, with 3 cell layers; surface papillose to microtomentose in section in between short fascicles. Apothecia hymenium to 135 µm tall. Algal layer extending to the margin of apothecium. Ascospores acicular, straight to sigmoid, 1(–3)-septate, 60–75 × 3 µm, ~20–25 times as long as broad.

Secondary chemistry. Gyrophoric acid and 4-O-methylgyrophoric acid.

Ecology and distribution. On hardwood trees in the Atlantic–Gulf Coastal Plain in North America, also known from the Antilles and reported from Panama (Büdel et al. 2000).

Comments. While *E. ravenelii* has been considered a synonym of *E. erosa* [*Sticta erosa*] by Tuckerman (1882) and other later authors, the two species can be clearly distinguished by some morphological features, such as the absence of pruina on the upper, more distinctly scrobiculate surface of the latter, as well as a different geographical distribution (North America and Greater Antilles versus South America, respectively). *Emmanuelia* (as *Lobaria*) *ravenelii* has been repeatedly reported from Brazil (Kalb 1983; Brako et al. 1985). The specimens distributed in Kalb's *Lichenes Neotropici* (No. 237) correspond to typical *E. erosa* and likely to other collections reported under this name from South America.

Specimens examined. DOMINICAN REPUBLIC. La Vega: 8.8 km N of Constanza, 6 km W of La Culata toward La Ciénaga de Bermudez; 5000 ft; pine woods along road and cut-over pines with *Pteridium* and shrubs and a few isolated pines; 28 April 1982, R. R. Harris (B, NY). USA. Alabama, Clebourne Co., Talladega National Forest, Shoal Creek, 33.733°N 85.560°W, alt. 400 m, forested hills, on hardwood bark, 2017 December 26, V. Charny 20171226-18 (CONN); Georgia, Candler Co., Charles Harold TNC Preserve, 0–0.25 mi N of Salem Church Rd., W side of Stocking Head Creek, 32.4169°, –82.0692°, bottomland mixed hardwood forest (*Nyssa*, *Acer*, *Quercus*) with pine (*Pinus*), on *Acer*, 2009 December 22, J. C. Lendemer 21774 (NY #1104321); Fifteenmile Creek Preserve, E side of Fifteenmile Creek just S of I-16, 32.3614°, –82.0325°, mesic hardwood forest (*Ilex*, *Nyssa*, *Fagus*, *Acer*, *Quercus*) with pine (*Pinus*) and cypress (*Taxodium*) on bluff, on *Magnolia virginiana*, 2009 December 22, J. C. Lendemer 21699 (NY #1149787); Effingham Co., Craig Barrow farm, 32.3526°, –81.4804°, north-aspect sand hill bluff, on bark, 2012 March 4, M. F. Hodges 8253 (NY #2057430); Emanuel Co., Ohoopce Dunes, 32.5253°, –82.4472°, on bark, 2007 October 7, M. F. Hodges 1941-C (NY #2057238); Tattall Co., Big Hammock Natural Area, blue and yellow trails, ~1 mi E of jct of CR 441 & GA 121/144/169, 31.8576°, –82.0589°, sand hill community with oak scrub and mixed hardwoods, on *Carya*, 2009 December 20, J. C. Lendemer 21443 (NY #1886944); Big Hammock Natural Area, ~1 mile southeast of Highway 121/144/169 off of Mack Phillips Road., 31.8636°, –82.0525°, alt. 20 m, dense forest with *Pinus palustris*, *Quercus* spp., and *Prunus* sp., on bark, 2013 March 25, T. S. Quedensley 10852 (NY #1150285); Mississippi, Wilkinson Co., 15 min. NW of St Francisville, between road 969 and the river, deep ravines with hardwood forest, on a deciduous tree in the bottom of the ravine, May 29 1976, E. Sérusiaux 1666 (LG); North Carolina, Craven Co., Croatan National Forest, 0–0.2 mi NE of FS 170, along tributary to Brices Creek, 1.9 mi NE of jct of FS170/FS121.2 and FS1101, 35.0369°, –77.0497°, alt. 4 m, swamp forest of mixed hardwoods (*Ilex*, *Acer*, *Nyssa*, *Liquidambar*, *Persea*, *Magnolia virginiana*), on *Acer*, 2013 March 5, J. C. Lendemer 35039 (NY #1865943); Dare Co., Alligator River National Wildlife Refuge, Brier Hall Rd. 0.25–0.5 mi S of jct w/ Mallard Rd., 0.25 mi N of US64, 35.8828°, –75.9375°, alt. 1 m, mixed hardwood (*Ilex opaca*, *Acer*, *Liquidambar*, *Nyssa*, *Persea*) – *Pinus* swamp with understory of *Cyrilla* and *Ilex glabra*, on *Acer*, 2014 March 21,

E. A. Tripp 4654 (NY #2203723); Dare Co., Alligator River National Wildlife Refuge, W of Whipping Creek Rd. 0.5 mi N of jct w/ Chip Rd., 35.6753°, –75.9625°, alt. 0 m, mature mixed hardwood (*Nyssa*, *Acer*, *Magnolia virginiana*, *Liquidambar*) – conifer (*Chamaecyparis* [dead], *Taxodium* and *Pinus*) swamp forest with *Ilex glabra* and *Clethra* understory, on large *Acer*, 2014 March 23, J. C. Lendemer 43114 (NY #2203643); Graham Co., Nantahala National Forest, W of Powell Branch at confluence with Fontana Lake, terminus of Cable Cove Road (CR 1287) at Cable Cove Boat Launch, 35.4372°, –83.7481°, alt. 527, stream ravine with acid hardwood-conifer forest, on poison ivy, 2016 March 18, R. C. Harris 61074 (NY #2467099); Washington Co., Bull Neck Swamp, Deep Creek Rd. 0.5 mi N of bridge over Deep Creek, 35.9372°, –76.3992°, alt. 0 m, mixed hardwood (*Nyssa*, *Acer*, *Magnolia virginiana*)–*Taxodium* swamp forest, on base of *Nyssa*, 2014 March 22, W. R. Buck 63035 (NY #2327942); South Carolina, McCormick Co., Sumter National Forest, Stevens Creek Heritage Preserve, N of SSR 88, ~1.5 mi NE of Clarks Hill, 33.6872°, –82.1614°, alt. 100 m, mesic mixed hardwood bluff forest, on rock, 2010 March 11, R. C. Harris 55880 (NY #1148729).

Molecular data. Yes.

Emmanuelia tenuis (Vain.) Lücking, Moncada & Gumboski, comb. nov. (Fig. 7B–C)

MycoBank MB 834655

Basionym: *Lobaria tenuis* Vain., Acta Soc. Fauna Fl. Fenn. 7(1): 199. 1890.

Types: Brazil, Minas Gerais: Sitio; 1000 m; 1885, Vainio 717 (TUR-V10691 – lectotype!; TUR-V10691a – isolectotype!; M-M0024301 – isolectotype!). Minas Gerais: Sitio; 1000 m; 1885, Vainio 727 (TUR-V10692 – paratype!; TUR-V10692a – paratype!).

≡ *Ricasolia tenuis* (Vain.) Stizenb., Flora 81: 111. 1895.

Diagnostic description. Primary photobiont a trebouxoid alga. Thallus medium-sized, rather closely adnate, composed of irregularly arranged to somewhat radiating lobes. Lobes intermediate, up to 7 mm wide, sinuose with rounded to truncate apices. Upper surface ± even, glabrous. Phyllidia abundant, marginal, elongate and usually branched. Lower surface thinly tomentose except for narrow, bare, whitish marginal zone, tomentum greyish brown. Apothecia rare, laminal, to 3 mm in diam., margin strongly prominent, shallowly to deeply crenulate. Ascospores acicular, straight to slightly curved or sigmoid, 1(–3)-septate, 55–70 × 3–3.5 μm, ~15–20 times as long as broad.

Secondary chemistry. Gyrophoric acid (major).

Comments. For a detailed discussion, see under *E. lobulifera* (above). The correct application of this name remains somewhat uncertain. In our phylogeny, specimens with marginal phyllidia are found in two different clades: one small separate clade (37504, 39705) and one larger clade intermingled with non-phyllidiate specimens identified as *E. elaeodes* (37502, 37544b, 40067). The two differ in the size and disposition of the phyllidia, which in the small separate clade are larger and oriented in the same direction as the lobes, and in the larger mixed clade are smaller and somewhat obliquely arranged. Both taxa were

found sympatric at one locality. Vainio's original material appears to correspond to the form with smaller, obliquely arranged phyllidia, which would mean that the separate clade, currently labeled aff. *tenuis*, requires a name.

Specimens examined. BRAZIL. Rio Grande do Sul: Caraá, Caraá Environmental Protection Area; 29°42'S, 50°17'W, 410 m; well-preserved Atlantic Forest fragment; 21 September 2014, Lücking 37502, 37544b (B, HAS). Santa Catarina: São Francisco do Sul, Parque Estadual Acarai; 26°16'S, 48°32'W, sea level; rather well preserved coastal Restinga forest; 8 October 2015, Lücking 40067 (B, JOI).

[aff. *tenuis*]. [Brazil] Espírito Santo: Santa Teresa, Estação Biológica de Santa Lúcia; 19°58'S, 40°32'W, 500–600 m; rather well preserved Atlantic Forest remnant; 28–30 September 2015, Lücking 39705 (B, ISE). Santa Catarina: São Francisco do Sul, Parque Estadual Acarai; 26°16'S, 48°32'W, sea level; rather well preserved coastal Restinga forest; 8 October 2015, Lücking 37504 (B, JOI).

Molecular data. Yes.

Key to the species of *Emmanuelia*

- 1 With laminal (to marginal) phyllidia; apothecia rare . . . 2
- 1 Without phyllidia; apothecia common 4
- 2(1) Phyllidia mostly laminal, shortly squamiform, unbranched to sparsely branched; lobe surface uneven to shallowly scrobiculate; southeastern North America . . . *E. lobulifera*
- 2(1) Phyllidia mostly marginal, elongate, much branched; lobe surface ±even; South America 3
- 3(2) Phyllidia rather large, oriented in the same way as the lobes *E. aff. tenuis*
- 3(2) Phyllidia smaller, obliquely oriented *E. tenuis*
- 4(1) Lobe underside becoming purplish red in the herbarium; lobes rather broad (5–10 mm), radiating, with rounded apices and ±even surface; apothecia small (1–2 mm), with entire to crenulate margins; South America *E. cuprea*
- 4(1) Lobe underside whitish to beige, with tomentum light to dark brown; lobes variable; apothecia larger (3–10 mm) 5
- 5(4) Medulla C– (lacking gyrophoric acid); lobes narrow (3–5 mm), irregularly arranged, with rounded to somewhat truncated apices and ±even surface; apothecia large (up to 10 mm diam.), with lobulate margins; South America *E. pseudolivacea*
- 5(4) Medulla C+ pinkish red (gyrophoric acid) 6
- 6(5) Lobe surface typically with numerous hemispherical, dendriscoauloid cephalodia; lobes narrow (3–5 mm), radiating, with rounded to somewhat truncated, crenulate to lobulate apices and uneven to shallowly scrobiculate surface; Galapagos, South America and southeastern North America *E. ornata*
- 6(5) Cephalodia internal if present 7
- 7(6) Ascospores 5-septate; thallus closely adnate, with very narrow lobes (up to 3 mm); Mexico *E. conformis*
- 7(6) Ascospores 1–3-septate; thallus closely to loosely adnate, with broader lobes (above 3 mm and to 20 mm) 8
- 8(7) Lobe surface shallowly to distinctly scrobiculate; lobes narrow (to 5 mm), ±radiating 9

- 8(7) Lobe surface ±even; lobes broader (5–20 mm), radiating to irregularly arranged 10
- 9(8) Lobe surface pruinose especially towards tips, shallowly scrobiculate; apothecia small (up to 3 mm), with entire to crenulate margins; southeastern North America, extending into the Greater Antilles. *E. ravenelii*
- 9(8) Lobe surface epruinose, distinctly scrobiculate; apothecia larger (up to 5 mm), with lobulate margins (flower-like); South America *E. erosa*
- 10(8) Lower tomentum forming a very regular dark brown, linear pattern except for abruptly bare marginal zone (similar to *Yoshimuriella*); apothecia with large lobules; Colombia *E. excisa*
- 10(8) Lower tomentum gradually thinning towards the margins, light to greyish brown, often with broader bare marginal zone; apothecia variable. 11
- 11(10) Apothecia medium-sized (3–5 mm), with entire to crenulate margins; lobes papery, intermediate (5–7 mm); South America *E. elaeodes*
- 11(10) Apothecia large (5–10 mm), with lobulate margins (flower-like); lobes leathery, broad (7–20 mm); South America 12
- 12(11) Lobes up to 12 mm broad, with numerous pycnidial warts on the surface; apothecia horizontal; ascospores up to 70 × 3 μm *E. americana*
- 12(11) Lobes up to 20 mm broad, lacking or with few pycnidial warts; apothecia obliquely oriented; ascospores up to 90 × 4 μm *E. patinifera*

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