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

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**Abstract.** The former family Lobariaceae, now included in Peltigerales 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 Lobarioideae. Emmanuelia currently comprises twelve species. It is superficially similar to the lobaroid genus Ricasola, but differs by its apothecia, rimmed by overarching and often crenulate to lobulate margins, with the paraphycium (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 lobaroid lichens can be applied to this group, and consequently a new name is proposed for this new genus, which is typified with *E. ravenelli* 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) ravenelli*.

**Key words:** Brazil, Dendriscocaulon, Lobarioideae, Neotropics, Peltigerales, Ricasola, taxonomy, USA

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**Introduction**

Recent years have witnessed major systematic rearrangements of lobaroid 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 phyllogenetics 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, lobaroid 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 (Avise & 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, lobaroid 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 lobaroid 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 *Ricasolina* (Moncada et al. 2013; Käffer et al. 2016; Lehnen et al. 2017; Etayo et al. 2018). Yoshimura (1998) treated the South American taxon as *L. quercizans* group, also implying a close relationship to *Ricasolina*. This group of lichens includes, among others, shade-loving species of the Atlantic Forest biome in South America such as *L. tenuis* (Käffer et al. 2009), as well as *L. ravenelii*, a well-known taxon 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 an 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; Widholm et al. 2019; Table 1). The final
dataset contained representatives of all known genera within the Lobaria 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 Guid-ance Web Server (Penn et al. 2010a, b; Sela et al. 2015). Sites with low-quality scores (i.e., with confidence scores

**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       |
|--------------------------|---------|----------|--------------------------|--------------|
| *Dendriscosticta* aff. *wrightii* | MT110113 | MT110145 | Groffinet 13074 (CONN)   | Taiwan       |
| *D. praetexta*           | MT110112 | MT110144 | LS Wang, HX Shi 14-46246 (KUN) | China        |
| *D. sp.*                 | MT110111 | MT110143 | Groffinet 13005 (CONN)   | Taiwan       |
| *Emmanuella aff. elaeodes* | MT110106 | MT110138 | Mercedo-Diaz 2939 (F)    | Dominician Republic |
| *E. aff. elaeodes*       | MT110082 | –        | Mercedo-Diaz 3526a (F)   | Jamaica      |
| *E. aff. ravenelii*      | MT110107 | MT110139 | Mercedo-Diaz 3031 (F)    | Dominician Republic |
| *E. aff. tenuis*         | MT110089 | MT110125 | Lücking 37504 (B, JOI)   | Brazil       |
| *E. americana*           | MT110098 | –        | Lücking 40112 (B, JOI)   | Brazil       |
| *E. elaeodes*            | MT110090 | MT110126 | Lücking 37511 (B, HAS)   | Brazil       |
| *E. elaeodes*            | MT110091 | MT110127 | Lücking 37544a (B, HAS)  | Brazil       |
| *E. elaeodes*            | MT110093 | MT110129 | Lücking 37546 (B, HAS)   | Brazil       |
| *E. elaeodes*            | MT110099 | –        | Lücking 40082 (B, JOI)   | Brazil       |
| *E. elaeodes*            | MT110087 | MT110123 | Spielmann 11214 (B, CGMS) | Brazil   |
| *E. erosa*               | MT110094 | MT110130 | Cáceres 25148 (B, ISE)   | Brazil       |
| *E. erosa*               | MT110097 | MT110133 | Mercedo-Diaz 3038c (F)   | Dominician Republic |
| *E. lobulifera*          | MT110076 | –        | Kaminski 18013 (NY)      | USA, Florida  |
| *E. lobulifera*          | MT110100 | –        | Lendemer 21578 (NY)      | USA, Georgia  |
| *E. lobulifera*          | MT110108 | MT110140 | Lendemer 41467 (NY)      | USA, South Carolina |
| *E. lobulifera*          | MT110075 | –        | Rosentreter 19739 (NY)   | USA, Florida  |
| *E. ornata*              | MT110085 | MT110121 | Moncada 8401 (B, CDS)    | Ecuador, Galapagos |
| *E. ornata*              | MT110086 | MT110122 | Moncada 8402 (B, CDS)    | Ecuador, Galapagos |
| *E. ornata*              | MT110109 | MT110141 | Rosentreter 17651 (NY)   | USA, Florida  |
| *E. ornata*              | MT110074 | –        | Rosentreter 20233 (NY)   | USA, Florida  |
| *E. patinifera*          | MT110101 | –        | Cáceres 25182 (B, ISE)   | Brazil       |
| *E. ravenelii*           | MT110105 | MT110137 | Buek 63035 (NY)          | USA, North Carolina |
| *E. ravenelii*           | MT110102 | MT110134 | Lendemer 34974 (NY)      | USA, North Carolina |
| *E. ravenelii*           | MT110103 | MT110135 | Quendedensley 10852 (NY) | USA, Georgia  |
| *E. ravenelii*           | MT110104 | MT110136 | Tripp 4654 (NY)          | USA, North Carolina |
| *E. tenuis*              | MT110088 | MT110124 | Lücking 37502 (B, HAS)   | Brazil       |
| *E. tenuis*              | MT110092 | MT110128 | Lücking 37544b (B, HAS)  | Brazil       |
| *E. tenuis*              | MT110095 | MT110131 | Lücking 40067 (B, JOI)   | Brazil       |
| *Lobaria isidiosa*       | MT110077 | MT110114 | LS Wang, HX Shi 14-46398 (KUN) | China |
| *L. isidiosa*            | MT110078 | MT110115 | LS Wang, HX Shi 14-46417 (KUN) | China |
| *L. linita*              | EU58809  | AB239702 | Högnaabba et al. (2009), Takahashi et al. (2006) – |
| *L. orientalis*          | MT110080 | MT110117 | LS Wang, HX Shi 14-45557 (KUN) | China |
| *L. orientalis*          | MT110079 | MT110116 | LS Wang, HX Shi 14-46123 (KUN) | China |
| *L. pulmonaria*          | AF609541 | AF129284 | Zoller et al. (1999)     | – |
| *L. retigera*            | MT110081 | MT110118 | Groffinet 13103 (CONN)   | Taiwan       |
| *L. retigera*            | AY124159 | AY124094 | Lohtander et al. (2002)  | – |
| *L. sachalinensis*       | EU58815  | AF524906 | Högnaabba et al. (2009), Stenroos et al. (2003) – |
| *Lobariella pallida*     | DQ912296 | HG650695 | Miadlikowska et al. (2006), Schmull et al. (2011) – |
| *L. pallidocrenulata*    | KC011075 | KC011051 | Moncada et al. (2013) – |
| *L. reticulata*          | KC011076 | KC011063 | Moncada et al. (2013) – |
| *L. subcresulata*        | DQ912297 | HG650696 | Miadlikowska et al. (2006), Schmull et al. (2011) – |
| *L. subxornata*          | EU558804 | AF524902 | Högnaabba et al. (2009), Stenroos et al. (2003) – |
| *Lobaria oregana*        | MT110083 | MT110119 | Riley 7/20/04 DNA vouch. 4 (NY) USA, Washington |
| *L. scrobiculata*        | AY340506 | AF350297 | Wiklund & Wedin (2003), Thomas et al. (2002) – |
| *L. silvae-vetersi*      | MT110084 | MT110120 | Goward 04-05 (UBC) Canada |
| *Ricasolia amplissima*   | AY340500 | AF524923 | Wiklund & Wedin (2003), Stenroos et al. (2003) – |
| *R. virens*              | MT110110 | MT110142 | Tønsberg 44757 (BG) Norway |
| *Sticta sublimbata*      | JQ736019 | JQ735986 | Magain et al. (2012) – |
| *S. sylvatica*           | KT281736 | KT281692 | Magain & Sérusiaux (2015) – |
| *Yoshimiuriella aff. subdissecta* | KC011073 | KC011029 | Moncada et al. (2013) – |
| *Y. dissecta*            | EU558808 | AF524920 | Högnaabba et al. (2009), Stenroos et al. (2003) – |
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. ravenelli, 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 ‘ucld.stdev’ parameter estimate) was close to zero. Consequently, a strict clock prior was applied. The dataset was analyzed with unlinked substitution 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 ‘ucld.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 Widhelm 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. ravenelli 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. ravenelli, 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 overarched 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 amphithecum (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
Emmanuelia paraplectenchymatous (Fig. 3C–D). A further difference is due to the photobiont layer stopping short below the parathecium and amphithecium are apically connected, in the three common species of Ricasolia the ascospores are as follows: 45–60 × 4–5 µm, ~9–12 times as long as broad (R. quercizans), 40–60 × 5–7 µm, ~7–9 times as long as broad (R. amplissima), and 25–45 × 6–10 µm, ~4–5 times as long as broad (R. virens). By contrast, for
sequenced species of *Emmanuelia* the following values were observed: 60–75 × 2.5–3 µm, ~20–25 times as long as broad (*E. ravenelii*), 60–80 × 2–3 µm, ~20–30 times as long as broad (*E. elaeodes*), 60–70 × 3–3.5 µm, ~15–20 times as long as broad (*E. tenuis*), and 50–80 × 2.5–4 µm, ~17–22 times as long as broad (*E. patinifera*). Somewhat similar measures, with length between 55 and 80 µm, width between 3 and 4 µm, 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 *Dendriscosticta*, *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*, *Lobaria*.

![Figure 2](image-url)
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 southeastern 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, ± 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-CGAATCATCGAATCTTTGAACGCACATTGCGCC-CCCYYGGYAC-3.

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**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 amphitheicum; C–D – E. ravenelii (Harris 14938) and E. elaeodes (Lücking 37544a), showing the parathecium apically separated from the amphitheicum by the photobiont layer. Scale = 100 μm.
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 dendriscocauloid 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 paratheciunm and amphitheciun 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 Maracá; 1400 m, 1885, Vainio 1187 (TUR-V10666 – lectotype!, here selected; MBT391290; M-M0207349 – isolectotype!).

**Diagnostic description.** Primary photobiont a trebouxiod 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.,
margin strongly prominent, lobulate. Ascospores acicular, straight to slightly curved, 1(–3)-septate, 60–80 × 2.5–3 µm, ~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 Acari; 26°16′S, 48°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°16′N, 48°25′W, 800 m; hilly, humid forest along stream; 23 July 1991, D. M. Vital & W. R. Buck 20429 (B).

Molecular data. Yes.
Emmanuela 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 treboux-oid alga. Thallus small, closely adnate, composed of ± radiating lobes. Lobes narrow, up to 3 mm wide, sinuose with undulate margins and rounded apices. Upper surface ± 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, 1(–3)-septate, 55–65 × 3.5–4 µm, ~15 times as long as broad.

Secondary chemistry. Gyrophoric acid (major).

Comments. This material was first considered conspecific with Emmanuela 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; Simpán 1993).

Molecular data. No.

Emmanuela 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 – islectotype!). [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 treboux-oid alga. Thallus medium-sized, rather closely adnate, composed of ± radiating lobes. Lobes intermediate, up to 10 mm wide, sinuose with rounded apices. Upper surface ± 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, 55–65 × 3.5–4 µm, ~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.

Emmanuela 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 treboux-oid alga. Thallus medium-sized, rather closely adnate, composed of ± radiating lobes. Lobes intermediate, up to 7 mm wide, sinuose with rounded to truncate apices. Upper surface ± 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, 3–5-septate, 70–80 × 2–3 µm, ~25–35 times as long as broad.

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

Comments. This material represents the genus Emmanuelia, a new genus of lobarioid lichen-forming fungi (A. Simon et al. 2017a). Therefore we consider R. intermedia a genuine member of that genus, whereas the Brazilian material represents the genus Emmanuela 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 multisepitate ascospores.

**Specimens examined.** BRAZIL. Rio Grande do Sul: Cariá, Cariá 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.) vuck., 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 medium-sized to large, closely adnate, composed of radiating lobes. Lobes intermediate, up to 10 mm wide, simose 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, laminar, 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.** Gyrrophoric acid (major).

**Comments.** This is a rather characteristic species, which in the past had been synonymized with *Emmanuelia* (as *Lobaria*) *ravenelli* 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: Itatiata National Park, Agulhas Negras road, km 8 on road to Agulhas Negras, 32 km NW of Itatiata, roadside; 22° 21′S, 44° 44′W, 2150 m; Atlantic Rain Forest, small roadside forest fragment near Aracuaria 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 Stränddünenschattenwald (Restinga); 29 September 1979, K. Kalb (B; distributed in *Lichenes Neotropici*, no. 237, as *Lobaria ravenelli*).

**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, MBF391292; 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, simose 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, laminar, 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.** Gyrrophoric 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. patinafera* 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 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′W, 72°54′06″; 3: 301. 1925.

**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!).
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 fascicules, 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 *E. 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), and the type, and *E. lobulifera* from the southeastern United States (e.g., Kaminski LK450, Lendemer 21578, 41467, and Rosenttreter 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, 31.1856°, −86.6728°, extensive limestone outcroppings, mesic hardwoods, on trunk of *Fagus*, 2007 April, 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 10th Street 2.2 mi E of FL 51 at Luvalville, 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 jet w/ E River Road, 31.9167°, −82.2681°, oak scrub with pine and occasional hardwoods, on *Lobaria*; 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., Otoopee 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 Otoopee River, 32.6028°, −82.4292°, oak scrub on white sand dunes grading into mixed hardwood forest, 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, Magnolia, Nyssa*) with NE aspect, on *Carya* base, 2009 December 21, J. C. Lendemer 21288 (NY #1150245); Tattnall Co., Big Hammock Natural Area, blue and yellow trails, ~1 mi E of jet of CR 441 & GA 121/144/169, 31.8576°, −82.0589°, sandhill community with oak scrub and mixed hardwoods, on *Quercus*, 2009 December 21, J. C. Lendemer 1467 (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 jet w/ FS 190, 33.2814°, −79.6244°, 20, upland mixed hardwood (*Acer, Quercus, Liquidambar, Ilex opaca, I. laevigata, Myrica*) and *Pinus* forest, on *Quercus*, 2013 December 6, J. C. Lendemer 41467 (NY #2327058).

**Molecular data.** Yes.

*Emmanuella 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 trebouxioiroid 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 lowly 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 dendriscocauloid cephalodia are reminiscent of those of *Ricascola* species, and since apothecia are apparently absent in this species, it cannot be readily assigned to *Emmanuella* without molecular data.

**Molecular data.** Yes.

*Emmanuella 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!).

≡ *Ricasalia 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.

≡ *Ricasalia casarettiana* (De Not.) Nyl., Acta Soc. Sci. Finn. 7(2): 438. 1863.

≡ *Lobaria casarettiana* (De Not.) Trevis., Lichenoth. Veneta: no. 75. 1869.

≡ *Ricasalia erosa var. casarettiana* (De Not.) Nyl., Flora 52: 314. 1869.
Flora 81: 112. 1895.

Emmanuelia ravenelii (Tuck.) Ant. Simon & Goffinet, comb. nov.  
Mycobank MB 834654

Basionym: Lobaria 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 – isotype!). 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 trebouxioide 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,
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 fascicules, 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 fascicules. 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. Glyrophoric acid and 4-O-methylglyrophoric 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. eros* [Sticta eros*] 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). *Emmanuellia* (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. eros* 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 Cienega 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, Cleburne 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 (as *Pyrenula*); Georgia, Walker 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 hill bluff, on bark, 2012 March 4, M. F. Hodges 8253 (NY #2057342); Emanuel Co., Ohoopee Dunes, 32.5253°, −82.4472°, on bark, 2007 October 7, M. F. Hodges 1941-C (NY #2057238); Tattnall Co., Big Hammock National 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 Caryya, 2009 December 20, J. C. Lendemer 21443 (NY #1886944); Big Hammock National Area, ~1 mile southeast of Highway 121/144/169 off of Mack Philips 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. Queensley 10852 (NY #1150285); Mississippi, Wilkinson Co., 15 mm. 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. Séruissiaux (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, 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.

*Emmanuellia tenuis* (Vain.) Lücking, Moncada & Gumboski, comb. nov. (Fig. 7B–C) MycoBank MB 834655

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

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

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

Diagnostic description. Primary photobiont a trebouxioïd 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, tumentum greyish brown. Apothecia rare, laminal, to 3 mm in diam., margin strongly prominent, shallowly to deeply crenulate. Asciopores aciculare, straight to slightly curved or sigmoid, 1(–3)-septate, 55–70 × 3–3.5 µm, ~15–20 times as long as broad.

Secondary chemistry. Glyrophoric 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-phyllidial 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).  

W, sea  

Caraá Environmental Protection Area; 29°42′S, 50°17′W, 500–600 m; rather well preserved coastal Restinga forest; 8 October 2015, Lücking 37504 (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  

| Key | Description | Reference |
|-----|-------------|-----------|
| 1   | With laminal (to marginal) phyllidia; apothecia rare | E. aff. tenuis |
| 2   | Without phyllidia; apothecia common | E. aff. tenuis |
| 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 | E. cuprea |
| 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 |
| 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) | E. erosa |
| 6(5) | Lobe surface typically with numerous hemispherical, dendriscocaulid 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 | E. ornata |
| 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) | E. conformis |
| 8(7) | Lobe surface shallowly to distinctly scrobiculate; lobes narrow (to 5 mm), ±radiating | E. erosa |

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