Epiphloea belongs to *Collemataceae* (Lecanoromycetes, lichenized Ascomycota)

Matthias SCHULTZ, Mats WEDIN, Henrike DIEL and Maria PRIETO

Abstract: The cyanolichen genus *Epiphloea* is currently included within the *Heppiaceae* (Lichinomycetes) based on ascus characteristics. The presumed presence of a prototunicate ascus has been used as support for this classification, despite the incongruence with other characters (e.g. spores). Here, we use a molecular phylogeny of the two markers mtSSU rDNA and *Mcm7* to investigate the position of *Epiphloea*. In addition, we have re-investigated the ascus characteristics. Our results place the two species, *Epiphloea byssina* and *E. terrena*, within the *Collemataceae*, nested in *Leptogium* s. str. The ascus type in both species is shown to be Lecanoralean and similar to the ascus in other *Collemataceae*, with a strongly amyloid tube-like structure. This observation supports the placement within Lecanoromycetes and refutes the earlier suggested affinities with *Heppiaceae* and Lichinomycetes. The correct names for these species are *Leptogium byssinum* and *Leptogium terrenum*.

Key words: cyanolichens, Leptogium, lichens, Lichinomycetes, phylogeny, systematics, taxonomy

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Introduction

Current progress in our understanding of the relationships among Ascomycota is substantial, and the recent advances in the phylogeny and evolution of lichen-forming Ascomycota associating with cyanobacteria is no exception (Schoch et al. 2009; Wedin et al. 2009, 2011; Otálora & Wedin 2013; Otálora et al. 2013, 2014; Spribille & Muggia 2013; Ekman et al. 2014; Magain & Sérusiaux 2014; Miądlikowska et al. 2014). Identifying and interpreting characters relevant for the classification of higher taxonomic ranks is a fundamental question in the phylogeneticsystematic study of the Ascomycota. Fungal classification is full of examples of groups where the current taxonomy is based on dubious observations erroneous or or interpretations of morphological structures. This is a problem which is particularly relevant for small and inconspicuous groups of cyanobacterial lichens.

During our ongoing studies of the phylogeny and character evolution of the Lichinomycetes, one of the largest remaining poorly understood groups of cyanobacterial lichens, a highly deviant genus was found to be Epiphloea, where the sequences of all molecular markers obtained were very different from other Lichinomycetes. Preliminary BLAST searches showed similarities with the Collemataceae, another group of cyanobacterial lichens. *Epiphloea* has for a long time been considered closely related to the Lichinomycete genus Heppia in Heppiaceae (Zahlbruckner 1924-1925; Eriksson 1999; Lumbsch & Huhndorf 2007), although they differ in spore characteristics and photobiont (i.e. Nostoc and muriform spores in Epiphloea, Scytonema and simple spores in Heppia). In the latest major treatment of Epiphloea, Jørgensen (2007) reported the asci to be prototunicate (thin-walled throughout and opening by apical rupturing), a common trait in Lichinomycetes. Jørgensen's statement, however, differs from earlier observations by Zahlbruckner (1919), who

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described the asci as having rounded and, at first, thickened tips that suggests a nonprototunicate ascus type.

The aim of this study is to clarify the phylogenetic placement of *Epiphloea*. To achieve this, we performed a phylogenetic analysis which included putative relatives based on DNA sequences of the mitochondrial SSU rDNA and the nuclear protein coding gene *Mcm7*. In order to re-evaluate and assess relevant morphological attributes, we studied the thallus and ascoma characteristics of both species in the genus, including type material, with particular focus on the ascus apex characteristics.

Material and Methods

Molecular study

For the phylogenetic study, we included three samples of Epiphloea and a wide selection of Collemataceae members (Table 1), representing all groups identified by Otálora et al. (2013, 2014). As in these previous studies, we used two members of Pannariaceae, Pannaria rubiginosa (Thunb. ex Ach.) Delise and Staurolemma omphalarioides (Anzi) P. M. Jørg. & Henssen, as outgroups rooting the tree with the latter. DNA was extracted using DNeasy Plant Mini Kit (Qiagen) and innuPREP Plant DNA Kit (Analytik Jena), according to the manufacturers' instructions. Amplifications were performed using 1:10 diluted DNA and with mtSSU1 and mtSSU3R (Zoller et al. 1999) primers for the mtSSU region. For amplification of the Mcm7 region, we used the primers Mcm7-709for and Mcm7-1348rev (Schmitt et al. 2009). When no bands were obtained in the PCR, we carried out a nested PCR using 1 µl of the PCR product and the internal primers Mcm7-CalicF and Mcm7-CalicR (Prieto et al. 2013).

PCR amplifications were performed using IllustraTM Hot Start Mix RTG PCR beads (GE Healthcare, UK) in a 25 µl volume, containing 3 µl of diluted genomic DNA, 10 µM of each primer and distilled water. Amplifications were performed using the following procedure: initial denaturation at 95 °C for 15 min, followed by 35 cycles of 95 °C for 45 s, 56 °C for 50 s, 72 °C for 1 min, followed by a final extension at 72 °C for 5 min. PCR products were subsequently purified using the enzymatic method Exo-sap-IT (USB Corporation, Santa Clara, California, USA) or spin columns (Geneaid Gel/PCR DNAFragments Extraction Kit). The purified PCR products were sequenced using the same amplification primers.

Sequences were assembled and edited using Sequencher v. 4.10.1. (Genes Codes Corporation, Ann Arbor) and deposited in GenBank (Table 1). These sequences were added to the *Collemataceae* alignment provided by Otálora *et al.* (2013), using MacClade 4.01 (Maddison & Maddison 2001) and adjusted and reduced manually. Ambiguous regions (*sensu* Lutzoni *et al.* 2000) and introns were delimited manually and excluded from the phylogenetic analyses.

Independent analyses were carried out in both data sets (i.e. mtSSU and Mcm7 alignments) using maximum likelihood-based inference (ML) in RAxML ver. 8.1.11 (Stamatakis 2014) and a GTRGAMMA model for tree inference. Bootstrapping was performed with a GTRCAT model and 1000 replicates. In order to check incongruence between the two analyses, we compared ML-BS individual gene trees, considering a conflict when a supported clade (bootstrap support >70%) for one marker was contradicted with significant support by another. Because no supported nodes were in conflict, the data were combined into a single data matrix. The combined maximum likelihood (ML) analyses were run with three distinct partitions (mtSSU, 1st and 2nd codon position for Mcm7 and the 3rd codon position for Mcm7), using the same settings as in the individual analysis.

We selected the best-fit models of nucleotide substitutions based on the Akaike Information Criterion (AIC) using jModeltest 0.1.1 (Posada 2008). The GTR model (Rodríguez *et al.* 1990) was selected for the three partitions, with a gamma distributed rate variation across sites with four categories and an estimated proportion of invariable sites. All parameters were unlinked, with rates allowed to vary across partitions under a flat Dirichlet prior.

The Bayesian inference was performed using MrBayes 3.2.3 (Ronquist *et al.* 2012). Two runs of 10 million generations, starting from an initial random tree and employing four simultaneous chains, were executed. A tree was saved every 100th generation. To ensure that stationarity and convergence were reached, to verify if mixing was appropriate, and choose a suitable burn-in, we plotted the log-likelihood values against the time generation with Tracer v.1.5.0 (Rambaut & Drummond 2007). A burn-in sample of 25 000 trees was discarded for each run. The remaining 150 000 trees (pooled from both independent runs) were used to estimate branch lengths and posterior probabilities (PPs). The analyses were run on the CIPRES Science Gateway v. 3.3 (Miller *et al.* 2010).

Selected specimens examined. Epiphloea byssina (Hoffm.) Henssen & P. M. Jørg. Germany: Baden-Württemberg: Heidelberg, W. v. Zwackh-Holzhausen (Lich. exs. 174) (UPS 111320 (L-62566)-neotype!; M-0154536, M-0154537-isoneotypes!). Bavaria: ad terram nudam prope Eichstadt [Eichstätt] in Bavaria, F. Arnold (Körber, Lich. Sel. Germ. 60; as Collema cheileum var. byssinum) (B).-Poland: Wojew. Dolnośląskie: Silesia, Hirschberg, auf Mauern, J. v. Flotow (Deutsch. Lich. 143A; as Collema cheileum var. byssaceum) (HBG).-Sweden: Uppland: Bondkyrko par., Norby, auf lehmigen Äckern, 7 vii 1920, G. Du Rietz (as f. obscurius Du Rietz) (B).-Norway: Oppland: Vågå municip., Nordherad, E of Svarthåmårbekken, by the parking lot just S of the road Fv454, on soil, 61.8674°N, 8.9886°E, 680 m, 30 vi 2013, M. Westberg (S F264803).-Russia: Sverdlovsk: Distr. Pervouralsk, Sloboda village, limestone outcrops on Chusovaya River, on soil, 2002, A. Paukov AGP20020804-02 (UFU) (dupl. hb. Schultz).

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L, fuscovirens (With.) Otálora et al. JX992923 JX992923 JX992923 L. undulatum (Flot.) Otálora et al. EU982554 JX99000 Leptogium azureum (Sw.) Mont. JX992942 JX992030 L. breitsomi Mont. JX992942 JX993004 L. breitsomi Mont. EU982553 JX993005 L. breitsomi Mont. EU982553 JX993007 L. breitsomi Mont. EU982553 JX993008 L. orticola (Taylor) Tuck. JX992944 JX993009 L. cyanseems (Rabenh.) Körb. EU982551 JX993008 L. denticulatum Nyl. 1 JX992944 JX993011 L. denticulatum Nyl. 2 JX992946 JX993011 L. denticulatum Nyl. 2 JX992947 JX993017 L. isdiosellum (Riddle) Sierk JX992950 JX993017 L. isdiosellum (Riddle) Sierk JX992955 JX993012 L. jacerides B. de Lesd. JX992956 JX993024 L. magnightum (B. de Lesd.) C. W. Dodge JX992957 JX993024 L. phyllocarpum (Pers.) Mont. 1 JX992966 - L. rieulare (Ach.) Mont. 2 JX9929266 - L. rieulare (Ach.) Mont. 2 <t< td=""><td>L. cristatum (L.) Otálora et al.</td><td></td><td>DQ917409</td><td>JX992979</td></t<>	L. cristatum (L.) Otálora et al.		DQ917409	JX992979
$ \begin{array}{llllllllllllllllllllllllllllllllllll$	L. fuscovirens (With.) Otálora et al.		JX992923	JX992983
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L. bicculare F. Wilson JX992042 JX993004 L. brissonii Mont. EU982583 JX993005 L. brissonii Mont. JX992044 JX993037 L. bissonii Mont. JX992044 JX993037 L. bissonii Mont. JX992044 JX993037 L. corticola (Taylor) Tuck. KT240180 KT240180 L. corticola (Taylor) Tuck. JX992045 JX993010 L. darytimum Tuck. JX992046 JX993011 L. denticulatum Nyl. 1 JX992046 JX993011 L. denticulatum Nyl. 2 JX992048 JX993011 L. digitatum (A. Massal.) Zahlbr. JX992048 JX993017 L isdicosellum (Riddle) Sierk JX992050 JX993017 L isdicosellum (Riddle) Sierk JX992054 JX993019 L laceroides B. de Lesd. JX992055 JX993012 L. marginellum (Sw.) Gray JX992056 JX993027 L. phyllocarpum (Pers.) Mont. 1 JX992056 JX993032 L. reviculare (Ach.) Mont. 2 JX992067 JX992067 L. reviculare (Ach.) Mont. 2 JX992067 JX992067 L. saturninum (Dicks.) Nyl. 1 JX992066 -	Leptogium azureum (Sw.) Mont.		JX992939	JX993002
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L. juressianum Tav. JX992954 JX993019 L. laceroides B. de Lesd. JX992955 JX993020 L. malmei P. M. Jørg. JX992956 JX993023 L. maginellum (Sw.) Gray JX992957 JX993024 L. papillosum (B. de Lesd.) C. W. Dodge JX992957 JX993027 L. phyllocarpum (Pers.) Mont. 1 EU982589 JX993028 L. phyllocarpum (Pers.) Mont. 2 EU982588 JX993031 L. resupinans Nyl. JX992964 JX993033 L. reiculatum Mont. JX992965 - L. saturninum (Dicks.) Nyl. 1 JX992965 - L. saturninum (Dicks.) Nyl. 1 EU982569 JX993034 L. sessile Vain. JX992967 JX993007 L. terrenum Nyl. 1 Portugal, van den Boom 41781 KT240181 (hb. van den Boom) L. tr240184 L. terrenum Nyl. 2 Portugal, Amieiro, Marques (PO) JX992972 L. velutinum P.M. Jørg. JX99205 JX993042 Paracollema italicum (B. de Lesd.) Otálora et al. 1 IX929272 JX993042	L. isidiosellum (Riddle) Sierk		JX992953	JX993018
L. laceroides B. de Lesd. JX992955 JX993020 L. malmei P. M. Jørg. JX992956 JX993023 L. marginellum (Sw.) Gray JX992957 JX993024 L. papillosum (B. de Lesd.) C. W. Dodge JX992957 JX993027 L. phyllocarpum (Pers.) Mont. 1 EU982588 JX993027 L. pseudofurfuraceum P. M. Jørg. & A. K. Wallace EU982582 JX993031 L. resupinans Nyl. JX992964 JX993038 L. rivulare (Ach.) Mont. 1 JX992965 - L. saturninum (Dicks.) Nyl. 1 JX992966 - L. saturninum (Dicks.) Nyl. 1 EU982569 JX993037 L. starurinum (Dicks.) Nyl. 1 EU982569 JX993037 L. starurinum Nyl. 2 Portugal, van den Boom) JX992967 - L. terrenum Nyl. 2 Portugal, Amieiro, Marques (PO) KT240182 KT240182 L. velutinum P.M. Jørg. AY360513 JX992927 JX993042 Pannaria rubiginosa (Thunb.) Delise AY360513 JX992925 JX992925 Paracollema italicum (B. de Lesd.) Otálora et al. 1 IX922925 JX992925 JX992924	L. juressianum Tav.		JX992954	JX993019
L. malmei P. M. Jørg. JX992956 JX992057 L. marginellum (Sw.) Gray JX992957 JX992057 L. papillosum (B. de Lesd.) C. W. Dodge JX992957 JX993027 L. phyllocarpum (Pers.) Mont. 1 EU982588 JX993028 L. phyllocarpum (Pers.) Mont. 2 EU982586 JX993028 L. pseudofurfuraceum P. M. Jørg. & A. K. Wallace EU982562 JX993031 L. resupinans Nyl. JX992963 JX992063 JX993033 L. reticulatum Mont. JX992965 - - L. rivulare (Ach.) Mont. 2 JX992065 - - L. saturninum (Dicks.) Nyl. 1 EU982569 JX993037 JX992067 - L. saturninum (Dicks.) Nyl. 2 AY340499 JX992067 JX993007 L. terrenum Nyl. 1 Portugal, van den Boom 47340499 JX992067 L. terrenum Nyl. 2 Portugal, Amieiro, Marques (PO) KT240182 KT240182 L. velutinum P.M. Jørg. JX99207 JX992061 JX992072 Pannaria rubiginosa (Thunb.) Delise AY36071 JX992925 JX992042 Paracollema italicum (B. de Lesd.) Otálora et al. 1 IX992925 IX992925	L. laceroides B. de Lesd.		JX992955	JX993020
L. marginellum (Sw.) Gray JX992957 JX992957 JX993024 L. papillosum (B. de Lesd.) C. W. Dodge JX992961 JX993027 L. phyllocarpum (Pers.) Mont. 1 EU982589 JX993028 L. phyllocarpum (Pers.) Mont. 2 EU982588 JX993029 L. psudofurfuraceum P. M. Jørg. & A. K. Wallace EU982562 JX993031 L. resupinans Nyl. JX992965 - L. rivulare (Ach.) Mont. 1 JX992965 - L. rivulare (Ach.) Mont. 2 JX992966 - L. saturninum (Dicks.) Nyl. 1 EU982569 JX993034 L. saturninum (Dicks.) Nyl. 2 AY340499 JX992967 L. terrenum Nyl. 1 Portugal, van den Boom) KT240181 KT240184 (hb. van den Boom) Portugal, Amieiro, Marques (PO) X992972 JX993041 L. velutimum P.M. Jørg. Ay360513 JX992925 JX992041 Paracollema italicum (B. de Lesd.) Otálora et al. 1 IX992925 JX992925 JX992925	L. malmei P. M. Jørg.		JX992956	JX993023
L. papillosum (B. de Lesd.) C. W. Dodge JX992061 JX993027 L. phyllocarpum (Pers.) Mont. 1 EU982589 JX993028 L. phyllocarpum (Pers.) Mont. 2 EU982588 JX993029 L. pseudofurfuraceum P. M. Jørg. & A. K. Wallace EU982562 JX993031 L. resupinans Nyl. JX992963 JX992963 JX993038 L. resupinans Nyl. JX992965 - - L. riculare (Ach.) Mont. 1 JX992966 - - L. rivulare (Ach.) Mont. 2 JX992966 - - L. saturninum (Dicks.) Nyl. 1 EU982569 JX993034 - L. saturninum (Dicks.) Nyl. 2 AY340499 JX992967 JX993007 L. terrenum Nyl. 1 Portugal, van den Boom KT240181 KT240184 (hb. van den Boom) - - Marques (PO) - L. velutimum P.M. Jørg. Portugal, Amieiro, Marques (PO) JX992972 JX993041 L. velutimum P.M. Jørg. JX99205 - - L. velutimum P.M. Jørg. JX99205 - - L. velutimum P.M. Jørg. JX99205 - - L. velutimum P.M. Jørg	L. marginellum (Sw.) Gray		JX992957	JX993024
L. phyllocarpum (Pers.) Mont. 1 EU982589 JX993028 L. phyllocarpum (Pers.) Mont. 2 EU982588 JX993029 L. pseudofurfuraceum P. M. Jørg. & A. K. Wallace EU982562 JX993031 L. resupinans Nyl. JX992963 JX993038 L. resupinans Nyl. JX992964 JX992065 L. rivulare (Ach.) Mont. 1 JX992966 - L. rivulare (Ach.) Mont. 2 JX992966 - L. saturninum (Dicks.) Nyl. 1 EU982569 JX993033 L. saturninum (Dicks.) Nyl. 1 EU982569 JX993035 L. sessile Vain. JX992967 JX993007 L. terrenum Nyl. 1 Portugal, van den Boom 41781 KT240181 KT240184 (hb. van den Boom) KT240182 KT240184 L. terrenum Nyl. 2 Portugal, Amiciro, Marques (PO) JX992972 JX993041 L. velutimum P.M. Jørg. JX99205 JX992042 JX992042 Paracollema italicum (B. de Lesd.) Otálora et al. 1 IX92225 IX992925	L. papillosum (B. de Lesd.) C. W. Dodge		JX992961	JX993027
L. phyllocarpum (Pers.) Mont. 2 EU982588 JX993029 L. pseudofurfuraceum P. M. Jørg. & A. K. Wallace EU982562 JX993031 L. resupinans Nyl. JX992963 JX993033 L. reticulatum Mont. JX992964 JX993038 L. rivulare (Ach.) Mont. 1 JX992965 - L. rivulare (Ach.) Mont. 2 JX992966 - L. saturninum (Dicks.) Nyl. 1 EU982569 JX993033 L. saturninum (Dicks.) Nyl. 1 EU982569 JX993035 L. sessile Vain. JX992967 JX993007 L. terrenum Nyl. 1 Portugal, van den Boom 41781 KT240181 KT240184 (hb. van den Boom) KT240182 KT240182 L. velutimum P.M. Jørg. Portugal, Amieiro, Marques (PO) JX992972 JX993041 L. velutimum P.M. Jørg. JX992925 JX992041 Paracollema italicum (B. de Lesd.) Otálora et al. 1 IX992925 JX992925	L. phyllocarpum (Pers.) Mont. 1		EU982589	JX993028
L. pseudofurfuraceum P. M. Jørg. & A. K. Wallace EU982562 JX993031 L. resupinans Nyl. JX992963 JX993033 L. reiculatum Mont. JX992964 JX993038 L. rivulare (Ach.) Mont. 1 JX992965 - L. rivulare (Ach.) Mont. 2 JX992966 - L. saturninum (Dicks.) Nyl. 1 EU982569 JX993034 L. saturninum (Dicks.) Nyl. 2 AY340499 JX993007 L. sessile Vain. JX992967 JX993007 L. terrenum Nyl. 1 Portugal, van den Boom 41781 KT240181 L. terrenum Nyl. 2 Portugal, Amieiro, Marques (PO) KT240182 KT240182 L. velutimum P.M. Jørg. JX992972 JX993041 Pannaria rubiginosa (Thunb.) Delise AY360513 JX992925 Paracollema italicum (B. de Lesd.) Otálora et al. 1 IX992925 IX992925	L. phyllocarpum (Pers.) Mont. 2		EU982588	JX993029
L. resupinans Nyl. JX992063 JX993033 L. reticulatum Mont. JX992064 JX993038 L. rivulare (Ach.) Mont. 1 JX992065 - L. rivulare (Ach.) Mont. 2 JX992066 - L. saturninum (Dicks.) Nyl. 1 EU982569 JX993033 L. saturninum (Dicks.) Nyl. 1 EU982569 JX993037 L. sessile Vain. JX992067 JX993007 L. terrenum Nyl. 1 Portugal, van den Boom KT240181 KT240184 (hb. van den Boom) KT240182 L. terrenum Nyl. 2 Portugal, Amieiro, Marques (PO) KT240182 L. velutinum P.M. Jørg. JX992972 JX993041 Pannaria rubiginosa (Thunb.) Delise AY360513 JX9920525 Paracollema italicum (B. de Lesd.) Otálora et al. 1 IX992925 IX992925	L. pseudofurfuraceum P. M. Jørg. & A. K. Wallace		EU982562	JX993031
L. reticulatum Mont.JX992064JX993038L. rivulare (Ach.) Mont. 1JX992065-L. rivulare (Ach.) Mont. 2JX992066-L. saturninum (Dicks.) Nyl. 1EU982569JX993034L. saturninum (Dicks.) Nyl. 2AY340499JX992067L. sessile Vain.JX922067JX993007L. terrenum Nyl. 1Portugal, van den BoomKT240181KT240181KT240184(hb. van den Boom)L. terrenum Nyl. 2Portugal, Amieiro, Marques (PO)KT240182L. velutinum P.M. Jørg.JX992057JX992072Pannaria rubiginosa (Thunb.) DeliseAY360513JX992042Paracollema italicum (B. de Lesd.) Otálora et al. 1IX92295IX992084	L. resupinans Nyl.		JX992963	JX993033
L. rivulare (Ach.) Mont. 1JX992965L. rivulare (Ach.) Mont. 2JX992966L. rivulare (Ach.) Mont. 2JX992966L. saturninum (Dicks.) Nyl. 1EU982569L. saturninum (Dicks.) Nyl. 2AY340499L. sessile Vain.JX992967L. terrenum Nyl. 1Portugal, van den Boom 41781L. terrenum Nyl. 2Portugal, Amieiro, Marques (PO)L. velutinum P.M. Jørg.JX992967Panaaria rubiginosa (Thunb.) DeliseAY360513Paracollema italicum (B. de Lesd.) Otálora et al. 1IX992925	L. reticulatum Mont.		JX992964	JX993038
L. rivulare (Ach.) Mont. 2 L. saturninum (Dicks.) Nyl. 1 L. saturninum (Dicks.) Nyl. 2 L. saturninum (Dicks.) Nyl. 2 L. sessile Vain. L. terrenum Nyl. 1 L. terrenum Nyl. 2 L. velutinum P.M. Jørg. Pannaria rubiginosa (Thunb.) Delise Paracollema italicum (B. de Lesd.) Otálora et al. 1 JX992966 - U. Velutinum P.M. Jørg. Paracollema italicum (B. de Lesd.) Otálora et al. 1 JX992967 JX993035 JX993037 Portugal, van den Boom 41781 (hb. van den Boom) Portugal, Amieiro, Marques (PO) JX992972 JX992972 JX993041 JX992955 JX992984	L. rivulare (Ach.) Mont. 1		JX992965	-
L. saturninum (Dicks.) Nyl. 1EU982569JX993034L. saturninum (Dicks.) Nyl. 2AY340499JX993035L. sessile Vain.JX992067JX993007L. terrenum Nyl. 1Portugal, van den Boom 41781KT240181L. terrenum Nyl. 2Portugal, Amieiro, Marques (PO)KT240182KT240182L. velutimum P.M. Jørg.JX992927JX993041Pannaria rubiginosa (Thunb.) DeliseAY360513JX992925JX992984Paracollema italicum (B. de Lesd.) Otálora et al. 1IX92295IX992984	L. rivulare (Ach.) Mont. 2		JX992966	-
L. saturninum (Dicks.) Nyl. 2AY340499JX993035L. sessile Vain.JX992967JX993007L. terrenum Nyl. 1Portugal, van den Boom 41781KT240181L. terrenum Nyl. 2Portugal, Amieiro, Marques (PO)KT240182L. velutimum P.M. Jørg.JX992972JX993041Pannaria rubiginosa (Thunb.) DeliseAY360513JX992925Paracollema italicum (B. de Lesd.) Otálora et al. 1IX992925IX992984	L. saturninum (Dicks.) Nyl. 1		EU982569	JX993034
L. sessile Vain.JX992967JX993007L. terrenum Nyl. 1Portugal, van den Boom 41781KT240181KT240184(hb. van den Boom)Portugal, Amieiro, Marques (PO)KT240182KT240182L. velutimum P.M. Jørg.JX992972JX993041Pannaria rubiginosa (Thunb.) DeliseAY360513JX993042Paracollema italicum (B. de Lesd.) Otálora et al. 1IX92295IX992984	L. saturninum (Dicks.) Nyl. 2		AY340499	JX993035
L. terrenum Nyl. 1Portugal, van den Boom 41781KT240181KT240184(hb. van den Boom)Portugal, Amieiro, Marques (PO)KT240182KT240182L. velutinum P.M. Jørg.JX992972JX993041Pannaria rubiginosa (Thunb.) DeliseAY360513JX993042Paracollema italicum (B. de Lesd.) Otálora et al. 1IX92295IX992984	L. sessile Vain.		JX992967	JX993007
L. terrenum Nyl. 2 Portugal, Amieiro, Marques (PO) L. velutinum P.M. Jørg. Pannaria rubiginosa (Thunb.) Delise Paracollema italicum (B. de Lesd.) Otálora et al. 1 Panaria rubiginosa (Thunb.) Delise	L. terrenum Nyl. 1	Portugal, <i>van den Boom</i> 41781 (hb. van den Boom)	KT240181	KT240184
L. velutimm P.M. Jørg. JX992972 JX993041 Pannaria rubiginosa (Thunb.) Delise AY360513 JX992092 Paracollema italicum (B. de Lesd.) Otálora et al. 1 IX992925 JX992984	L. terrenum Nyl. 2	Portugal, Amieiro, Maraues (PO)	KT240182	KT240185
Pannaria rubiginosa (Thunb.) Delise AY360513 JX993042 Paracollema italicum (B. de Lesd.) Otálora et al. 1 IX992925 IX992984	L. velutinum P.M. Jørg.		IX992972	IX993041
Paracollema italicum (B. de Lesd.) Otálora et al. 1 IX992925 IX992984	Pannaria rubiginosa (Thunh.) Delise		AY360513	IX993042
	Paracollema italicum (B. de Lesd.) Otálora et al. 1		JX992925	JX992984

TABLE 1. GenBank accession numbers for specimens used in this study. New sequences are indicated by accession numbers in bold.

TABLE 1. Co	ntinued
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Species	Voucher specimen	GenBank A	GenBank Acc. number	
		mtSSU	Mcm7	
P. italicum (B. de Lesd.) Otálora et al. 2		JX992926	JX992985	
Pseudoleptogium diffractum (Körb.) Müll. Arg.		JX992949	JX993015	
Rostania multipunctata (Degel.) Otálora et al.		JX992930	JX992988	
R. occultata (Bagl.) Otálora et al.		JX992931	JX992990	
Scytinium biatorinum (Nyl.) Otálora et al.		JX992940	JX993003	
S. fragrans (Sm.) Otálora et al.		JX992922	JX992981	
S. lichenoides (L.) Otálora et al.		DQ923120	JX993021	
S. magnussonii (Degel. & P. M. Jørg.) Otálora et al.		EU982565	JX993022	
S. palmatum (Huds.) Gray 1		JX992959	JX993025	
S. palmatum (Huds.) Gray 2		JX992960	JX993026	
S. parvum (Degel.) Otálora et al.		JX992933	JX992992	
S. plicatile (Ach.) Otálora et al.		GQ259033	JX993030	
S. pulvinatum (Hoffm.) Otálora et al.		EU982590	JX993032	
S. schraderi (Bernh.) Otálora et al.		EU982559	JX993036	
S. turgidum (Ach.) Otálora et al.		EU982592	JX993040	
Staurolemma omphalarioides (Anzi) P. M. Jørg. & Hensser	L	EU982560	JX993043	

Epiphloea terrena (Nyl.) Trevis. France: Languedoc-Roussillon, Dept. Pyrénées Orientales: Colliour, Pla de las Fourques, in fossa arcis Fortrand, 5 vii 1872, W. Nylander (H-NYL 42806-lectotype!). Provence-Alpes-Côte d'Azur, Dept. Vaucluse: Vaucluse, Morières, Plateau de Gadagne, ad terram argillaceo-sabulosum secus viam im vicinitate Querceti ilicis, 12 ii 1971, G. Clauzade & C. Roux (Vězda, Lich. sel. exs. 987) (W 1975-261).—Portugal: Norte, Distr. Vila Real: Amieiro, terricolous on side of dust road, UTM 29TPF 3471, 7 iii 2012, J. Marques (PO) (HBG DNA no. 3731); Vale do Moinho, terricolous on side of dirt road, 7 iii 2012, J. Marques (PO) (dupl. hb. M. Schultz 17149). Centro, Distr. Coimbra: Ribeira de Relvas, 2011, J. Marques 686 (PO) (dupl. hb. M. Schultz 17150). Algarve, Distr. Faro: NE of Albufeira, c. 7 km ENE of Paderne, along new road from Espargal to the south, W slope of small hill, low calcareous outcrops and a few Ceratonia siliqua trees, terricolous, 37.214°N, 8·1202°W, 235 m, 2009, P. van den Boom 41781 (hb. P. van den Boom) (HBG DNA 3707).-Spain: Canary Islands: Tenerife, NW, near Buenavista del Norte, road to La Costa and Punta de la Laja, coastal scrub with Euphorbia spp., ± exposed soil crust, 28.375°N, 16.833°W, 50 m, 2001, M. Schultz 17083e (hb. M. Schultz).

Heppia despreauxii (Mont.) Tuck. USA: Arizona: Cochise Co., c. 2 km S of Tombstone, soil over calcareous rock, 1999, M. Schultz 16097a (hb. M. Schultz).

Results

A total of six sequences were generated for this study (Table 1). The combined data set consisted of 69 taxa and 1227 unambiguously aligned sites, 663 for the mtSSU and 564 for the *Mcm7*.

Maximum likelihood analyses resulted in a single most likely tree with an ln-likelihood of $-13452 \cdot 12$. The harmonic mean ln-likelihood from the Bayesian analysis was $-13968 \cdot 6$. The tree topologies obtained by the maximum likelihood and the Bayesian approaches did not show any significant conflict (Fig. 1).

Discussion

Here we show that *Epiphloea* clearly belongs within the *Collemataceae*. This is not surprising as the *Epiphloea* species were classified in *Collema* or *Leptogium* when they were originally described and are very similar to other *Collemataceae* (sensu Wedin et al. 2009)

FIG. 1. Phylogenetic position of *Epiphloea* within the family *Collemataceae*. Best tree from RAxML with bootstrap support (ML-BS) and posterior probabilities (PP) obtained in the Bayesian analysis. * Indicates a support value of 100% for ML-BS and 1 for PP. Supported clades by both analyses (ML-BS > 70, PP > 0.95) are marked with thicker black branches and with thicker grey branches when the node is only supported by one of the two analyses.



and Otálora et al. 2013) in morphology (i.e. thallus structure, photobionts and ascospores; Fig. 2). Pycnidia have not been reported previously in the two Epiphloea species nor have we succeeded in seeing them. Contrary to some recent suggestions, our observations of type and other material showing that the asci in *Epiphloea* are Lecanoralean, with well-developed apical domes and distinct tube-like amyloid apical structures similar to other Collemataceae (Fig. 3A-C). This observation is clearly supported by the phylogenetic relationship found here. In contrast, the asci are always thin-walled in Heppiaceae (Fig. 3D), where Epiphloea used to be classified. It should be noted, however, that juvenile asci of Epiphloea are sometimes still thin-walled due to incomplete development, whereas the mature asci observed by us always had amyloid apical structures. Thus the phylogenetic placement is also supported by the ascus apex characters.

Both Epiphloea species are part of Leptogium s. str. (sensu Otálora et al. 2014), and both already have names coined in this genus. Leptogium s. str. chiefly contains corticolous species with a few exceptions such as Leptogium cyanescens (corticolous to saxicolous) or L. britannicum (growing on coastal soils). Leptogium byssinum (Hoffm.) Zwackh ex Nyl. and L. terrenum Nyl. are two further examples of non-corticolous, soil dwelling species in the newly circumscribed genus. Furthermore, the thallus anatomy, especially in L. terrenum, adds to the variability of the genus by including species with a \pm paraplechtencymatous thallus (otherwise found in some species of Scytinium). On the other hand, both species share the typical eucortex of Leptogium: a single layer of isodiametric cells in L. byssinum (Fig. 3F) and two to three rows of isodiametric cortex cells in L. terrenum (Fig. 3E).

Leptogium byssinum and L. terrenum form the sister clade to Leptogium rivulare, L. crispatellum and L. biloculare, a relationship which is not so easy to explain. Difficulties in the interpretation may be due to a still incomplete taxon sampling. Leptogium rivulare has an unique ecology, growing on seasonally submerged exposed roots, soil or occasionally on rock along the margins of sluggish rivers

and ponds. Leptogium crispatellum is an epiphyte known only from New Zealand. Leptogium biloculare is an epiphytic species occurring in moist, montane to subalpine regions in Australia. The three species seem to form a natural group within Leptogium s. str., but their molecular relationship with *Epiphloea* is not obviously corroborated by morphological and anatomical evidence. It rather seems that Leptogium byssinum and L. terrenum form a group within Leptogium s. str., with preference for disturbed and dry soil habitats combined with an otherwise somewhat unusual thallus anatomy. The general similarity in overall macro-morphology of L. byssinum and L. terrenum to species of Heppia (Lichinomycetes) is likely to be the result of parallel evolution, as these distinctly unrelated taxa have adapted to similar environmental conditions in dry soils where they form part of biological soil crusts.

Nomenclatural Summary

Leptogium (Ach.) Gray nom. cons. prop. (Jørgensen *et al.* 2013)

Epiphloea Trevis., Rendiconti Reale Ist. Lombardo Sci., ser.
2 13(3): 73 (1880) syn. nov.; type: E. terrena (Nyl.) Trevis.
Amphidium Nyl., Lich. Pyren. Orient.: 72 (1891) nom.
illeg., non Schimp. 1856 (bryophytes, nom. cons.); type: Amphidium terrenum (Nyl.) Nyl.

Leptogium byssinum (Hoffm.) Zwackh ex Nyl.

Actes Soc. Linn. Bordeaux 21: 270 (1857); Epiphloea byssina (Hoffm.) Henssen & P. M. Jørg., Nordic Lich. Fl. 3: 144 (2007) syn. nov.

The following description largely follows that given by Jørgensen (1994), but according to our observations the asci are Lecanoralean with a distinct apical dome and a strongly amyloid tube-like structure (Fig. 3C).

Thallus forming a thin crust over bare soil breaking up into irregularly shaped areoles up to 3 mm in size, consisting of brownish granules that sometimes become increasingly dissolved into bluish, leprose granules resembling soralia (Fig. 2D), or it remains \pm crustose and corticate (Fig. 2C), attached to the substratum by pale rhizohyphae. *Photobiont* layer with short chains of *Nostoc* and



FIG. 2. A & B, Leptogium terrenum; A, olivaceous, small-squamulose thallus, apothecia adnate, with dark red discs (Marques s. n., dupl. hb. M. Schultz 17149); B, apothecia with distinct proper exciple (Marques 686, dupl. hb. M. Schultz 17150). C & D, Leptogium byssinum; C, dark olivaceous, crustose thallus, with semi-immersed apothecia (Flotow, Deutsch. Lich. 143A, HBG); D, thallus almost entirely dissolved into leprose, bluish (olive) granules, apothecia with brownish discs (Paukov AGP20020804-02, dupl. hb. M. Schultz). Scales = 1 mm. In colour online

densely reticulate to paraplectenchymatous hyphae. *Medulla* absent, upper and lower cortex composed of a single row of isodiametric cells, $4.5-8.0 \times 4-6 \,\mu m$ in size.

Apothecia circular, immersed to semiimmersed, rarely adnate, up to 2 mm diam.; disc dark reddish to brownish, initially concave, later plane, surrounded by thin thalline margin which becomes obscured in sorediate thallus parts (Fig. 2C & D). *Hymenium* 100–150 μ m high, KOH/IKI + blue; *proper exciple* laterally thin, up to 10 μ m thick, composed of ellipsoid to elongated cells, 5–8 × 3·0–3·5 μ m, exciple apically thickened, cells roundish, 8·0–11·5 × 7–9 μ m, pale reddish brown-coloured, sub-hymenial layer 30–40 μ m high; *paraphyses*



FIG. 3. A–D, asci stained with Lugol's solution after pretreatment with KOH. A & B, *Leptogium terrenum*, ascus with amyloid, tube-like apical structure (Vězda, Lich. sel. 987, W 1975-261); C, *Leptogium byssinum*, like A & B, but with muriform ascospores (Körber, Lich. sel. 60, B); D, *Heppia despreauxii*, thin-walled, prototunicate ascus not staining with iodine, ascospores simple (*Schultz* 16097a, hb. Schultz); E, *Leptogium terrenum*, thallus cross-section showing upper cortex of isodiametric cells, photobiont layer with densely reticulate, vertically elongated cells (*Marques* s. n., dupl. hb. M. Schultz 17149); F, *Leptogium byssinum*, thallus granule surrounded by single-row cortex, photobiont layer with densely reticulate hyphae (Du Rietz, B). Scales = 10 µm. In colour online.

simple, straight, $1-2 \mu m$ thick, terminal cells slightly enlarged. *Asci* narrowly clavate, $60-100 \times 10-15 \mu m$ in size, 8-spored, Lecanoralean, with a distinct amyloid tube-like apical structure. *Ascospores* hyaline, ellipsoid, muriform, $16-28 \times 7-15 \mu m$. Pycnidia unknown.

Leptogium terrenum Nyl.

Flora 56: 195 (1873); Epiphloea terrena (Nyl.) Trevis., Rendiconti Reale Ist. Lombardo Sci., ser. 213(3): 73 (1880) syn. nov.; Amphidium terrenum (Nyl.) Nyl., Lich. Pyren. Orient.: 72 (1891) syn. nov.

Thallus resembling Heppia, with smaller irregularly shaped squamules; thallus subcrustose, (vellowish) olive, 0.4-1.2 mm wide, tightly to loosely adpressed (Fig. 2A), often divided into small lobules 0.4-0.8 mm in size, up to 150 µm thick, pale below, attached to the substratum by robust, pale rhizohyphae that are indistinctly separated from the photobiont layer and composed of 1-2 rows of relatively large, isodiametric cells 10-15 µm in size. Photobiont layer with short chains of Nostoc and mostly vertically arranged, reticulate hyphae composed of elongated cells (Fig. 3E). Medulla absent, lower cortex usually inconspicuous (obscured by rhizohyphae), with 1–2 rows of small, \pm isodiametric cells, $5.0-7.5 \,\mu\text{m}$ in size.

Apothecia circular, at first semi-immersed, soon adnate, 0.6-0.9 mm diam.; disc reddish to reddish brown, widely exposed (Fig. 2B). Hymenium 100–125 µm high, KOH/IKI+ blue; proper exciple distinct, hyaline, composed of small cells of $5-10 \times 3-5 \,\mu\text{m}$, subhymenial layer up to 100 µm thick (medial sections!); paraphyses simple, straight, 1.5-2.0 µm thick, terminal cells slightly enlarged. Asci narrowly clavate, $80-90 \times 11-22 \,\mu\text{m}$, 8-spored, Lecanoralean with a distinct amyloid tube-like apical structure (Fig. 3A & B). Ascospores hyaline, muriform, $15-26 \times 9.5-12.0 \,\mu\text{m}$.

Pycnidia unknown.

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