



Reallocation of foliicolous species of the genus *Strigula* into six genera (lichenized Ascomycota, Dothideomycetes, Strigulaceae)

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Abstract

Strigula sensu lato has been previously defined based on phenotype characters as a rather broad genus including tropical to temperate species growing on a wide array of substrata. In this study, based on a multilocus phylogenetic approach, we show that foliicolous species form six well-delimited clades that correlate with diagnostic phenotype features, including thallus morphology, carbonization of the involucrellum and excipulum, ascospore dimensions, and type of macroconidia. Given the topology, with five of the six clades emerging on long stem branches, and the strong phenotypical differentiation between the clades, we recognize these at the genus level, making mostly use of previously established genus names. Four genera, namely *Phylloporis*, *Puiggariella*, *Raciborskiella*, and *Racoplaca*, are resurrected for the *S. phyllogena*, *S. nemathora*, *S. janeirensis*, and *S. subtilissima* groups, respectively, whereas one new genus, *Serusiauxiella* gen. nov., is introduced for a novel lineage with peculiar macroconidia. The only sequenced non-foliicolous species, *S. jamesii*, is not closely related to these six foliicolous lineages but clusters with *Flavobathelium* and *Phyllobathelium*, revealing it as an additional undescribed genus-level lineage being treated elsewhere. Within the new genus *Serusiauxiella*, three new species are described: *Serusiauxiella filifera* sp. nov., *S. flagellata* sp. nov., and *S. sinensis* sp. nov. In addition, ten new combinations are proposed: *Phylloporis austropunctata* comb. nov., *P. radiata* comb. nov., *P. vulgaris* comb. nov., *Puiggariella confluens* comb. et stat. nov., *P. nemathora* comb. nov., *P. nigrocincta* comb. nov., *Racoplaca maculata* comb. nov., *R. melanobapha* comb. nov., *R. transversoundulata*, and *R. tremens* comb. nov. We also report on a peculiar, previously unrecognized growth behaviour of the macroconidial appendages in *Strigula* s.lat.

Keywords *Cephaleuros* · Epiphyllous lichens · Generic classification · Higher taxa · Macroconidial appendages · *Phycopeltis* · Surface fixation · *Trentepohlia*

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Introduction

The genus *Strigula* s.lat. in the family *Strigulaceae* (Order *Strigurales*) comprises about 70 species (Hyde et al. 2013; Lücking et al. 2017). *Strigula* was first mentioned as a *nomen nudum* in a summary of the lichen system by Fries (1821), with reference to his *Systema Mycologicum* 2 years later, where Fries gave a short description (Fries 1823). It is generally assumed that Fries at that time did not include a species, and therefore Santesson (1952) selected *S. smaragdula* Fr. as type, a name established by Fries 7 years later (Fries 1830). In the protologue, Fries (1823: 535) explicitly cited the name *Endocarpon smaragdulum* (“... sed ob thallum lobatulum *Endocarpi smaragduli* facie inter Lichenes locatum”). The latter name had been previously introduced as *E. smaragdulum* Wahlenb. in Acharius (1803) and corresponds to an unrelated, saxicolous lichen currently known as *Myriospora smaragdula* (Wahlenb.) Nägeli ex Uloth. It is unlikely that Fries identified his material with that species, and the least nomenclaturally disruptive interpretation is that Fries made a simply comparison and did not give the foliicolous taxon a name. Hence the later introduced name *Strigula smaragdula* (Fries 1830) indeed is to be considered the first established name for this species.

Numerous species currently included in *Strigula* s.lat. were described posterior to Fries (e.g. Fée 1825; Montagne 1845; Santesson 1952; Hawksworth et al. 1980; Harris 1995; Aptroot et al. 2003; Roux and Sérusiaux 2004; Lücking 2008; McCarthy 2009a). A detailed modern account of most of the foliicolous species was given in the monograph for *Flora Neotropica* (Lücking 2008). The separate family *Strigulaceae* was introduced by Zahlbruckner (1898) for an array of partly unrelated pyrenocarpus lichens growing on leaves. Eriksson (1982) and Vězda (1984) restricted the family to three genera, *Strigula*, *Phylloporis* and *Raciborskiella*, a classification followed in some other works (e.g. Llaens 2003). Species assigned to *Raciborskiella* grow exclusively on the leaf underside, whereas species assigned to *Phylloporis* (and previously to *Porina*) are supracuticular (Santesson 1952; Vězda 1984). The subcuticular foliicolous species classified in *Raciborskiella* and *Strigula* thereby associate with photobionts in the genus *Cephaleuros* (*Trentepohliaceae*), a semiparasitic alga which obtains carbohydrates through photosynthesis but other nutrients from the host leaves (Nelson 2008; Brooks et al. 2015). While *Cephaleuros* appears to represent a phylogenetically coherent entity, it is nested within a broadly defined genus *Trentepohlia* s.lat. whose generic delimitation remains unresolved (Nelsen et al. 2011a; Zhu et al. 2014). However, these ecological differences were not accepted as being sufficient for generic delimitation,

and both *Phylloporis* and *Raciborskiella* were included in *Strigula* (Harris 1975, 1995), a classification accepted in major works (Roux and Sérusiaux 2004; Lücking 2008; McCarthy 2009a; Lücking et al. 2017).

With this broadened generic concept, *Strigula* s.lat. was further emended by adding numerous corticolous and saxicolous species (Hawksworth et al. 1980; Etayo 1993; Harris 1995; McCarthy 1995, 1997, 2001, 2009a, b; McCarthy and Malcolm 1996; Roux and Sérusiaux 2004). Notably, the only non-foliicolous species thus far sequenced, the saxicolous *Strigula jamesii* (Swinsc.) R.C. Harris, was first described in the genus *Geisleria* and only later transferred to *Strigula* (Harris in Hawksworth et al. 1980). The type of *Geisleria*, *G. sychnogonoides* Nitschke, has been shown through molecular and morphological study to be an apotheciate taxon close to *Stictidaceae* and entirely unrelated to *Strigulaceae* (Aptroot et al. 2014). Hence the name *Geisleria* is not available as genus name for non-foliicolous species of *Strigula* s.lat. including *S. jamesii*.

Strigulaceae have been analysed molecularly in various studies, including their higher level phylogenetic relationships (Nelsen et al. 2009, 2011b) and species delimitation in foliicolous representatives (Jayalal et al. 2013; Krishnamurthy and Subramanya 2016; Jiang et al. 2016, 2017a, b; Krishnamurthy and Kumar 2017). However, to date no broader systematic study of the genus based on molecular data has been carried out. Adding to the somewhat diffuse delimitation of the genus, Harris (1995) even suggested merging *Phyllobathelium* with *Strigula*, while other workers kept this genus separate (Aptroot et al. 1997; Lücking 2008; McCarthy 2009a) or placed it in a separate family, *Phyllobatheliaceae* (Eriksson et al. 2004; Eriksson 2005). Molecular data (Nelsen et al. 2009) supported the inclusion of *Phyllobatheliaceae* within *Strigulaceae*, but clearly separate from foliicolous lineages of *Strigula*. Two new genera, *Phyllocratera* and *Flavobathelium*, were also added to the family (Aptroot et al. 1997; Lücking et al. 1997; Nelsen et al. 2009). Further, the non-lichenized *Oletheriostrigula* (Huhndorf and Harris 1996) was transferred to *Strigulaceae* (Lücking et al. 2017), but based on macroconidial morphology, this placement is not justified. A recent systematic and phylogenetic analysis of some *Porina*-like foliicolous lichens resulted in the recognition of a novel lineage forming a new family, *Tenuitholiascaceae*, sister to *Strigulaceae* in *Strigurales* (Jiang et al. 2020).

In this study, we provide the first broad-scale multilocus phylogeny of *Strigula* s.lat. focusing on foliicolous taxa, employing markers from the rDNA (ITS, nuSSU, nuLSU) and protein-coding loci (TEF1- α , RPB2). The results prompted us to reclassify foliicolous taxa into six well-delimited genera.

Materials and methods

Material examined

A total of 65 specimens of *Strigulales* belonging to 27 species from included for the ingroup taxon set, representing material from the Americas (Brazil, Cuba, Guatemala) and Asia (China). Additional material from other regions (Costa Rica, Australia) was included for morphological comparison. Specimens examined (and duplicates) are preserved in the Fungarium-Lichenarium of the Institute of Microbiology, Chinese Academy of Sciences (HMAS-L), the herbarium of the Botanischer Garten und Botanisches Museum und Botanischer Garten Berlin (B), the Australian National Herbarium, Centre for Australian National Biodiversity Research (CANB), and the herbarium of the Jardín Botánico Nacional de Cuba in Havana (HAJB).

Morphological observations

For morphological and anatomical studies, a LEICA M125 dissecting microscope (Leica Microsystems, Singapore) and a Zeiss Axioscope2 compound microscope (Carl Zeiss, Göttingen) were used. Photographs were taken with an AxioCam MRc5 connected to a Zeiss Imager A2-M2 microscope (Carl Zeiss, Göttingen) for microscopic features. Thin-layer chromatography (TLC) (Orange et al. 2001) was employed for the detection of lichen substances in selected specimens. Features of the ascus apex were examined using Lugol's solution, without pre-treatment by KOH (Baral 1987).

Molecular phylogeny of the mycobiont

The modified CTAB method (Rogers and Bendich 1988) was used for DNA extraction. DNA, suspended in ddH₂O, was amplified by the polymerase chain reaction (PCR). The nuclear ribosomal RNA gene region, including internal transcribed spacers (ITS) 1 and 2 and the 5.8S subunit, was amplified using the primer pair ITS5 and ITS4 (White et al. 1990). Partial nuclear ribosomal small subunit (nuSSU) sequences were amplified using combinations of the following, mostly *Strigulales*-specific primers: SF5 (Jiang et al. 2020), SR5 (Jiang et al. 2020), and SR3 (newly designed here; Table 1). A portion of the fungal nuclear ribosomal large subunit (nuLSU) was amplified using combinations of the primers ITS3 (White et al. 1990), LR72 (Jiang et al. 2020), and LR71, 28SR4R, 28BYF1, and NEWR2 (newly designed here; Table 1). Partial TEF1- α sequences were generated using

Table 1 Newly designed, *Strigulales*-specific primers for the nuSSU and nuLSU rDNA regions

Primer acronym	Primer sequence
SR3	GCTGCGTTCTTCATCGTTGC
LR71	TACTACCACCAAGATCTGC
28SR4R	TTTCTGGCACCTCTAGCCTC
28BYF1	ATGAAGAACGCGGCAAAATG
NEWR2	CTAAACCCAGCTCACGTTCC

the primers TEF1a-983-F (Rehner and Buckley 2005) and TEF1a-1567R-HTL (Nelsen et al. 2011b). The second largest subunit of the RNA polymerase II (RPB2) was amplified using the primers fRPB2-5F and fRPB2-7cR (Liu et al. 1999).

PCR reactions were carried out in 25 μ l reaction volume and the components used were 2 μ l total DNA, 1 μ l each primer (10 μ M), 12.5 μ l 2 $\times$ Taq MasterMix, 8.5 μ l ddH₂O. Amplification was performed using a Biometra T-Gradient thermal cycler. Cycling parameters of LSU, ITS and SSU were set to an initial denaturation at 95 °C for 5 min, followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at 54 °C for 30 s, extension at 72 °C for 1 min, and a final extension at 72 °C for 10 min. PCR amplifications of TEF1- α were initiated with a 2 min denaturation at 94 °C. The annealing temperature in the first amplification cycle was 66 °C, which was subsequently incrementally reduced by 1 °C per cycle over the next 9 cycles. An additional 30 amplification cycles were then performed, each consisting of 30 s denaturation at 94 °C, a 30 s annealing step at 56 °C, and a 1 min extension at 72 °C, concluding with a 10 min incubation at 72 °C (Rehner and Buckley 2005). The PCR conditions of RPB2 included: initial denaturation at 95 °C for 5 min; 35 cycles of 1 min at 95 °C, 2 min at 50 °C, an increase of 1 °C/5 s to 72 °C, and 2 min at 72 °C; and a 10-min incubation at 72 °C (Liu et al. 1999). The PCR products were checked on 0.8% agarose electrophoresis gels stained with ethidium bromide and then sent to the sequencing facilities of Majorbiology Cooperation, China, for sequencing. Sequences were deposited in GenBank (Table 2).

New sequences generated for each locus were first analyzed separately with other sequences obtained from GenBank (Table 2). Sequences of each marker were aligned using MAFFT 7.402 (Kato and Toh 2010) and analysed separately (see below) to evaluate potential conflicts. Conflicts were evaluated manually by comparing the topology and position of each of the major clades in relation to their topology and position in the concatenated analysis (see Results).

ML trees were reconstructed for each individual marker and for a concatenated data set including the nuSSU, nuLSU,

Table 2 Voucher information and GenBank accession numbers for specimens of *Strigulales* used in the molecular phylogenetic analyses

Species	DNA extract	Country	Collector	ITS	nuLSU	nuSSU	TEF1- α	<i>RPB2</i>
<i>Flavobathelium epiphyllum</i>	MPN-67			–	GU327717	JN887382	JN887423	–
<i>Phyllobathelium anomalum</i>	MPN-242			–	GU327722	JN887386	JN887430	–
<i>Phylloporis</i> cf. <i>obducta</i>	HMAS-L0139218	China	S.H. Jiang	–	MN720034	MN727002	MN738504	MN738529
<i>Phylloporis</i> cf. <i>obducta</i>	HMAS-L0139247	China	S.H. Jiang	–	MN720035	MN727003	MN738505	MN738530
<i>Phylloporis</i> cf. <i>obducta</i>	HMAS-L0139286	China	S.H. Jiang	–	MN720036	MN727004	MN738506	MN738531
<i>Phylloporis</i> cf. <i>obducta</i>	HMAS-L0139339	China	X.L. Wei & S.H. Jiang	–	MN720037	MN727005	MN738507	MN738532
<i>Phylloporis</i> cf. <i>obducta</i>	HMAS-L0139635	China	S.H. Jiang	–	MN720038	MN727006	MN738508	MN738533
<i>Phylloporis</i> <i>phyllogena</i>	ISE-33944	Brazil	A. B. Xavier Leite	–	MN720039	MN727007	MN738509	MN738534
<i>Puiggariella nemathora</i>	ISE-32586	Brazil	A. B. Xavier Leite	–	–	MN727009	MN738510	–
<i>Puiggariella nemathora</i>	ISE-32794	Brazil	A. B. Xavier Leite	–	–	MN727008	–	MN738535
<i>Puiggariella nigro-cincta</i>	HMAS-L0139335	China	X.L. Wei & S.H. Jiang	–	MN720040	MN727010	MN738511	MN738536
<i>Puiggariella nigro-cincta</i>	HMAS-L0139350	China	X.L. Wei & S.H. Jiang	–	MN720041	MN727011	MN738512	MN738537
<i>Puiggariella nigro-cincta</i>	HMAS-L0141541	China	X.L. Wei & S.H. Jiang	–	MN720042	MN727012	MN738513	MN738538
<i>Raciborskiella janei-rensis</i>	HMAS-L0130589	China	J.H. Wang & R.D. Liu	–	MN720043	MN727013	MN738514	—
<i>Raciborskiella talaumae</i>	HMAS-L0139624	China	S.H. Jiang	–	MN720044	MN727014	MN738515	–
<i>Raciborskiella talaumae</i>	HMAS-L0139627	China	S.H. Jiang	–	MN720045	MN727015	MN738516	–
<i>Racoplaca melanobapha</i>	HMAS-L0139331	China	X.L. Wei & J.H. Wang	–	MN720046	MN727016	MN738517	MN738539
<i>Racoplaca melanobapha</i>	HMAS-L0139623	China	S.H. Jiang	–	MN720047	MN727017	MN738518	MN738540
<i>Racoplaca subtilissima</i>	ISE-32602	Brazil	A. B. Xavier Leite	–	–	MN727018	MN738519	–
<i>Serusiaxiella filifera</i> sp. nov.	HMAS-L0130625	China	J.H. Wang & R.D. Liu	MN720009	–	–	–	–
<i>Serusiaxiella filifera</i> sp. nov.	HMAS-L0130627	China	J.H. Wang & R.D. Liu	MN720010	–	–	–	–
<i>Serusiaxiella filifera</i> sp. nov.	HMAS-L0130629	China	J.H. Wang & R.D. Liu	MN720011	MN720048	MN727019	MN738520	MN738541
<i>Serusiaxiella filifera</i> sp. nov.	HMAS-L0139219	China	S.H. Jiang	MN720019	–	–	–	–
<i>Serusiaxiella filifera</i> sp. nov.	HMAS-L0139223	China	S.H. Jiang	MN720020	–	–	–	–
<i>Serusiaxiella filifera</i> sp. nov.	HMAS-L0139234	China	S.H. Jiang	MN720022	–	–	–	–
<i>Serusiaxiella filifera</i> sp. nov.	HMAS-L0139270	China	X.L. Wei & J.H. Wang	MN720012	–	–	–	–
<i>Serusiaxiella filifera</i> sp. nov.	HMAS-L0139272	China	X.L. Wei & J.H. Wang	MN720013	–	–	–	–

Table 2 (continued)

Species	DNA extract	Country	Collector	ITS	nuLSU	nuSSU	TEF1- α	<i>RPB2</i>
<i>Serusiauxiella filifera</i> sp. nov.	HMAS-L0139288	China	S.H. Jiang	MN720021	–	–	–	–
<i>Serusiauxiella filifera</i> sp. nov.	HMAS-L0139298	China	S.H. Jiang	MN720015	–	–	–	–
<i>Serusiauxiella filifera</i> sp. nov.	HMAS-L0141639	China	S.H. Jiang	MN720014	–	–	–	–
<i>Serusiauxiella filifera</i> sp. nov.	HMAS-L0141641	China	S.H. Jiang	MN720016	–	–	–	–
<i>Serusiauxiella filifera</i> sp. nov.	HMAS-L0141644	China	S.H. Jiang	MN720017	–	–	–	–
<i>Serusiauxiella filifera</i> sp. nov.	HMAS-L0141648	China	S.H. Jiang	MN720018	MN720049	MN727020	MN738521	MN738542
<i>Serusiauxiella filifera</i> sp. nov.	HMAS-L0141656	China	S.H. Jiang	MN720023	MN720050	MN727021	MN738522	MN738543
<i>Serusiauxiella filifera</i> sp. nov.	HMAS-L0141660	China	S.H. Jiang	MN720024	–	–	–	–
<i>Serusiauxiella flagellata</i> sp. nov.	HMAS-L0130554	China	J.H. Wang & R.D. Liu	MN720025	–	–	–	–
<i>Serusiauxiella flagellata</i> sp. nov.	HMAS-L0141609	China	J.H. Wang & R.D. Liu	MN720026	–	–	–	–
<i>Serusiauxiella flagellata</i> sp. nov.	HMAS-L0139216	China	J.H. Wang & R.D. Liu	MN720027	–	–	–	–
<i>Serusiauxiella sinensis</i> sp. nov.	HMAS-L0141605	China	J.H. Wang & R.D. Liu	MN720033	–	–	–	–
<i>Serusiauxiella sinensis</i> sp. nov.	HMAS-L0141611	China	J.H. Wang & R.D. Liu	MN720031	MN720053	MN727022	MN738525	MN738546
<i>Serusiauxiella sinensis</i> sp. nov.	HMAS-L0141612	China	J.H. Wang & R.D. Liu	MN720032	–	–	–	–
<i>Serusiauxiella sinensis</i> sp. nov.	HMAS-L0141614	China	J.H. Wang & R.D. Liu	MN720030	–	–	–	–
<i>Strigula acuticonidiarum</i>	HMAS-L0138045			–	MK206236	MK206217	MK273083	MK273111
<i>Strigula antillarum</i>	B-600205084	Cuba	R. Lücking et al.	–	MN720054	–	MN738526	MN738547
<i>Strigula</i> cf. <i>atrocarpoides</i>	HMAS-L0139342	China	X.L. Wei & S.H. Jiang	–	MN720055	MN727023	MN738527	MN738548
<i>Strigula dispersa</i>	HMAS-L0137212			–	MN720056	–	MK273097	MK273125
<i>Strigula guangxiensis</i>	HMAS-L0138040			–	MK206256	–	MK273103	MK273131
<i>Strigula guangxiensis</i>	HMAS-L0138041			–	MK206257	–	MK273104	MK273132
<i>Strigula jamesii</i>	MPN-548			–	JN887404	JN887388	JN887432	–
<i>Strigula</i> cf. <i>macaronesica</i>	HMAS-L0130615			–	MK206251	MK206230	MK273098	MK273126
<i>Strigula</i> cf. <i>macaronesica</i>	HMAS-L0139260			–	MK206252	MK206231	MK273099	MK273127
<i>Strigula macrocarpa</i>	HMAS-L0139289			–	MK206241	MK206222	MK273088	MK273116
<i>Strigula macrocarpa</i>	HMAS-L0141394			–	MK206240	MK206221	MK273087	MK273115
<i>Strigula nitidula</i>	HMAS-L0139358			–	MN788374	MN788375	MN793983	MN793982
<i>Strigula prasina</i>	B-600205026	Guatemala	R. Lücking et al.	–	–	MN727024	MN738528	–
<i>Strigula sinoaus-tralis</i>	HMAS-L0137204			–	MK206249	–	MK273096	MK273124
<i>Strigula smaragdula</i>	HMAS-L0138066			KY100296	–	–	–	–
<i>Strigula smaragdula</i>	HMAS-L0138068			KY100299	–	–	–	–

Table 2 (continued)

Species	DNA extract	Country	Collector	ITS	nuLSU	nuSSU	TEF1- α	<i>RPB2</i>
<i>Strigula</i> cf. <i>smaragdula</i>	HMAS-L0139166			–	MK206235	MK206216	MK273082	MK273110
<i>Strigula</i> cf. <i>smaragdula</i>	HMAS-L0141395			–	MK206234	MK206215	MK273081	MK273109
<i>Strigula</i> cf. <i>smaragdula</i>	HMAS-L0141396			–	MK206233	MK206214	MK273080	MK273108
<i>Strigula univelbise- rialis</i>	HMAS-L0137657			–	MK206243	MK206224	MK273090	MK273118
<i>Strigula univelbise- rialis</i>	HMAS-L0137658			–	MK206245	MK206226	MK273092	MK273120
<i>Strigula univelbise- rialis</i>	HMAS-L0137659			–	MK206242	MK206223	MK273089	MK273117
<i>Strigula univelbise- rialis</i>	HMAS-L0137660			–	MK206244	MK206225	MK273091	MK273119
<i>Tenuitholiascus porinoides</i>	HMAS-L0139638			–	MK206259	MK352441	MK273106	MK273134
<i>Tenuitholiascus porinoides</i>	HMAS-L0139639			–	MK206258	MK352442	MK273105	MK273133
<i>Tenuitholiascus porinoides</i>	HMAS-L0139640			–	MK206260	MK352443	MK273107	MK273135

Newly generated sequences are indicated in boldface

TEF- α , and *RPB2*. For the individual markers and the concatenated data set, we analysed two taxon sets, a broader one encompassing related *Dothideomycetes* (Table 3) and a narrower one focusing on *Strigulales* (Table 2). For this, we used IQ-TREE 1.6.6 (Nguyen et al. 2015) with 1000 bootstrap pseudoreplicates. The best-fit substitution model was selected using ModelFinder (Kalyaanamoorthy et al. 2017): TIM2 + F + I + G4 was selected as the best model for the *Dothideomycetes* taxon set, and TNe + I + G4 for the *Strigulales* taxon set. For the ITS alignment, TN + F + G4 was selected as the best model.

Bayesian analysis was performed with MrBAYES assuming the general time reversible model including estimation of invariant sites and a discrete gamma distribution with six rate categories (GTR + I + G), for the single-genes and the combined analyses (Ronquist et al. 2012). A run with 5,000,000 generations and employing 20 simultaneous chains was executed. Posterior probabilities above 90% and bootstrap support above 50% are considered significant supports. Analyses of the single markers and the combined data set resulted in basically the same topology.

Phylogenetic trees were drawn using FigTree 1.4.2 (Rambaut 2012). Alignments were submitted to TreeBase (<http://purl.org/phylo/treebase/phyloids/study/TB2:S26015>).

Molecular phylogeny of the photobiont

Photosymbionts of selected specimens were also analyzed phenotypically and molecularly. ITS nrDNA sequences

of the algal partners were amplified using the primers nr-SSU-1780-59 and nr-LSU-0012-39 (Piercey-Normore and Depriest 2001). The newly generated sequences were submitted to GenBank and aligned with fourteen samples of *Trentepohliaceae* from GenBank representing the three major lichenized genera currently distinguished in that family (Table 4).

The resulting alignment was subjected to randomized accelerated maximum likelihood in RAXML 8 with 1000 pseudoreplicates (Stamatakis 2014), using the GTR-GAMMA model chosen by JModeltest (Felsenstein 1985; Posada 2008) and otherwise with default parameters.

Results

Molecular phylogeny of the mycobiont

Comparison between the individual markers and the concatenated data set revealed topological variation (Table 5). The *Phylloporis* and *Raciborskiella* clades were monophyletic and strongly supported in all instances (no *RPB2* data for the latter); its position varied according to marker but this variation was not supported. The *Puiggariella* and *Racoplaca* clades were also consistently recovered as monophyletic with strong support (somewhat lower support for the first in TEF1- α). In these cases, however, nuLSU showed a supported conflict for *Puiggariella* with *RPB2* and the concatenated data set, whereas *Racoplaca* exhibited a supported

Table 3 GenBank accession numbers for other sequences used in the molecular phylogenetic analyses

Species	LSU	SSU	TEF1- α	RPB2
<i>AcrospERMum adeanum</i>	EU940104	EU940031	–	EU940320
<i>AcrospERMum compressum</i>	EU940084	EU940012	–	EU940301
<i>AcrospERMum gramineum</i>	EU940085	EU940013	–	EU940302
<i>Aigialus grandis</i>	GU301793	GU296131	–	GU371762
<i>Aigialus parvus</i>	GU301795	GU296133	GU349064	GU371771
<i>Aliquandostipite khaoyaiensis</i>	GU301796	AF201453	GU349048	FJ238360
<i>Anisomeridium ubianum</i>	GU327709	JN887379	–	–
<i>Apiosporina collinsii</i>	GU301798	GU296135	GU349057	–
<i>Aquasubmersa japonica</i>	LC061588	LC061583	LC194385	LC194422
<i>Arthopyrenia salicis</i>	AY538339	AY538333	–	–
<i>Ascocratera manglicola</i>	GU301799	GU296136	–	GU371763
<i>Asterina cesticola</i>	GU586215	GU586209	–	–
<i>Asterina fuchsiae</i>	GU586216	GU586210	–	–
<i>Asterina phenacis</i>	GU586217	GU586211	–	–
<i>Asterina weinmanniae</i>	GU586218	GU586212	–	–
<i>Asterina zanthoxyl</i>	GU586219	GU586213	–	–
<i>Aureobasidium pullulans</i>	DQ470956	DQ471004	DQ471075	DQ470906
<i>Botryobambusa fusicoccum</i>	JX646809	JX646826	–	–
<i>Botryosphaeria agaves</i>	JX646808	JX646825	–	–
<i>Botryosphaeria dothidea</i>	DQ678051	DQ677998	DQ767637	DQ677944
<i>Delitschia didyma</i>	DQ384090	AF242264	–	–
<i>Delitschia winteri</i>	DQ678077	DQ678026	DQ677922	DQ677975
<i>Dendrographa decolorans</i>	AY548815	AY548809	DQ883725	DQ883715
<i>Dothidea hippophaeos</i>	DQ678048	U42475	DQ677887	DQ677942
<i>Dothidea insculpta</i>	DQ247802	DQ247810	DQ471081	AF107800
<i>Dothidea sambuci</i>	AY544681	AY544722	DQ497606	KT216559
<i>Dothiora cannabinae</i>	DQ470984	DQ479933	DQ471107	DQ470936
<i>Dyfronomyces rhizophorae</i>	GU479799	GU479766	GU479860	–
<i>Dyfronomyces tiomanensis</i>	KC692156	KC692155	KC692157	–
<i>Elsinoe centrolobi</i>	DQ678094	DQ678041	DQ677934	–
<i>Elsinoe phaseoli</i>	DQ678095	DQ678042	DQ677935	–
<i>Elsinoe veneta</i>	DQ767658	DQ767651	DQ767641	–
<i>Falciformispora lignatilis</i>	GU371826	GU371834	GU371819	–
<i>Fal. senegalensis</i>	KF015627	KF015634	KF015688	KF015716
<i>Fal. tompkinsii</i>	KF015625	KF015640	KF015685	KF015718
<i>Gibbera conferta</i>	GU301814	GU296150	GU349041	–
<i>Glioniopsis praelonga</i>	FJ161195	FJ161154	FJ161103	FJ161113
<i>Glonium circumserpens</i>	FJ161200	FJ161160	FJ161108	FJ161126
<i>Glonium stellatum</i>	FJ161179	FJ161140	FJ161095	–
<i>Hysteropatella clavispora</i>	AY541493	DQ678006	DQ677901	DQ677955
<i>Jahnula aquatica</i>	EF175655	EF175633	–	–
<i>Jahnula bipileata</i>	EF175657	EF175635	–	–
<i>Kirschsteiniothelia aethiops</i>	AY016361	AY016344	DQ677884	DQ470914
<i>Kirschsteiniothelia lignicola</i>	HQ441568	HQ441569	–	–
<i>Lecanactis abietina</i>	AY548812	AY548805	–	DQ987635
<i>Lepidosphaeria nicotiae</i>	DQ678067	–	DQ677910	DQ677963
<i>Lichenocodium aeruginosum</i>	HQ174269	–	–	–
<i>Lichenocodium erodens</i>	HQ174267	–	–	–
<i>Lichenocodium lecanorae</i>	HQ174263	–	–	–
<i>Lichenocodium usneae</i>	HQ174265	–	–	–
<i>Lichenothelia calcarea</i>	KC015061	KC015081	–	–

Table 3 (continued)

Species	LSU	SSU	TEF1- α	<i>RPB2</i>
<i>Lichenothelia convexa</i>	KC015068	KC015083	–	–
<i>Lindgomyces breviappendiculata</i>	AB521748	AB521733	–	–
<i>Lindgomyces ingoldianus</i>	AB521736	AB521719	–	–
<i>Lophiotrema neoarundinaria</i>	AB524596	AB524455	AB539110	AB539097
<i>Macrophomina phaseolina</i>	DQ678088	DQ678037	DQ677929	KX463996
<i>Massariosphaeria grandispora</i>	GU301842	GU296172	GU349036	GU371725
<i>Massariosphaeria typhicola</i>	GU301844	GU296174	–	GU371795
<i>Megalotremis verrucosa</i>	GU327718	JN887383	–	–
<i>Microthyrium microscopicum</i>	GU301846	GU296175	GU349042	GU371734
<i>Microxyphium aciculiforme</i>	GU301847	GU296176	GU349045	GU371736
<i>Microxyphium theae</i>	GU301849	GU296178	GU349060	–
<i>Myriangium duriaei</i>	DQ678059	AY016347	DQ677900	DQ677954
<i>Myriangium hispanicum</i>	GU301854	GU296180	GU349055	GU371744
<i>Mytilinidion resinicola</i>	FJ161185	FJ161145	–	–
<i>Mytilinidion scolecosporum</i>	FJ161186	FJ161146	FJ161102	FJ161121
<i>Natipusilla bellaspora</i>	JX474863	JX474868	–	–
<i>Natipusilla decorospora</i>	HM196369	HM196376	–	–
<i>Natipusilla limonensis</i>	HM196370	HM196377	–	–
<i>Natipusilla naponensis</i>	HM196372	HM196379	–	–
<i>Neofusicoccum parvum</i>	AY928045	EU673151	–	FJ900618
<i>Neofusicoccum ribis</i>	DQ678053	DQ678000	DQ677893	EU339554
<i>Oedohysterium insidens</i>	GQ221882	GU323190	–	GU371785
<i>Ophiosphaerella sasicola</i>	AB524599	AB524458	AB539111	AB539098
<i>Phaeotrichum benjaminii</i>	AY004340	AY016348	DQ677892	DQ677946
<i>Phyllosticta citricarpa</i>	GU301815	GU296151	GU349053	KY855864
<i>Pseudotetratloa curviappendiculata</i>	AB524608	AB524467	–	–
<i>Rasutoria tsugae</i>	EF114705	EF114730	–	–
<i>Roccella fuciformis</i>	AY584654	AY584678	–	KF036046
<i>Roccella montagnei</i>	GU138014	AF110341	–	DQ987665
<i>Roussoella hysteroioides</i>	AB524622	AB524481	AB539115	AB539102
<i>Roussoella pustulans</i>	AB524623	AB524482	AB539116	AB539103
<i>Sydowia polyspora</i>	DQ678058	DQ678005	DQ677899	DQ677953
<i>Trichodeliitschia bisporula</i>	GU348996	GU349000	GU349020	GU371802
<i>Trichodeliitschia munkii</i>	DQ384096	DQ384070	–	–
<i>Triplosphaeria maxima</i>	AB524637	AB524496	–	–
<i>Ulospora bilgramii</i>	DQ678076	DQ678025	DQ677921	DQ677974
<i>Venturia inaequalis</i>	GU301878	GU296204	GU349023	–
<i>Westerdykella cylindrica</i>	AY004343	AY016355	DQ497610	–
<i>Westerdykella ornata</i>	GU301880	GU296208	GU349021	GU371803

conflict in the nuSSU with the nuLSU and the concatenated data set. The *Serussiauxiella* clade was also consistently monophyletic with strong support, but supported conflict was detected between TEF1- α , *RPB2* and the concatenated data set.

Finally, the *Strigula* s.str. clade was recovered as monophyletic with strong support in the nuSSU, *RPB2* and the concatenated data set, but paraphyletic in the nuLSU and polyphyletic in TEF1- α (Table 5). In the latter case, the subclades behaving aberrantly were the *S. nitidula* and the *S.*

prasina clades. Given that in 22 of 24 instances, including the concatenated data set, the six clades resulted monophyletic and with strong support, we use the concatenated tree as phylogenetic hypothesis for this group and interpret the few supported conflicts as the result of conflicting individual gene histories in the cases of the protein-coding markers. The few observed conflicts between the nuSSU and nuLSU cannot be attributed to individual gene histories, as both form part of the rDNA cistron that is expected to evolve in tandem. While these conflicts, and the resulting short

Table 4 Voucher information and GenBank accession numbers for specimens of used for the molecular phylogenetic analyses of *Trentepohliaceae* photobionts

Species	DNA extract	ITS
<i>Cephaleuros expansus</i>	GD1318	KX586811
<i>Cephaleuros karstenii</i>	DZ1309	KX586781
<i>Cephaleuros karstenii</i>	DZ1312	KX586784
<i>Cephaleuros</i> sp. from <i>Strigula</i> sp.	HMAS–L0130622	MK211171
<i>Cephaleuros</i> sp. from <i>Strigula</i> cf. <i>smaragdula</i>	HMAS–L0141395	MK211172
<i>Phycopeltis aurea</i>	YN1220 (IHB)	KP067280
<i>Phycopeltis prostrata</i>	YN1218 (IHB)	KP067283
<i>Phycopeltis</i> sp. from <i>Teniotholiascus porinoides</i>	HMAS–L0139638	MK211174
<i>Phycopeltis</i> sp. from <i>Teniotholiascus porinoides</i>	HMAS–L0141346	MK211173
<i>Phycopeltis</i> sp. from <i>Phylloporis</i> cf. <i>obducta</i>	HMAS–L0139220	MN718160
<i>Phycopeltis</i> sp. from <i>Phylloporis</i> cf. <i>obducta</i>	HMAS–L0139228	MN718161
<i>Phycopeltis</i> sp.	YN1202	KP067279
<i>Trentepohlia</i> sp. from <i>Serusiauxiella filifera</i> sp. nov.	HMAS–L0130629	MN718162
<i>Trentepohlia</i> sp. from <i>Serusiauxiella flagellata</i> sp. nov.	HMAS–L0139216	MN718163
<i>Trentepohlia</i> sp. from <i>Serusiauxiella flagellata</i> sp. nov.	HMAS–L0130554	MN718164
<i>Trentepohlia</i> sp. from <i>Serusiauxiella sinensis</i> sp. nov.	HMAS–L0141614	MN718165
<i>Trentepohlia</i> sp.	DS22	KC489115
<i>Trentepohlia</i> sp.	SAG118.80	KM020078
<i>Trentepohlia</i> sp.	TreF154	KC489121
<i>Ulva tepida</i>	PR18	KT374011

Newly generated sequences are indicated in boldface

branches in the concatenated backbone, make it challenging to evaluate the exact relationships between the six clades, they do not affect their interpretation as distinct phylogenetic entities.

For the *Dothideomycetes* taxon set, the concatenated alignment contained 4371 characters (1272 for nuLSU, 1176 for nuSSU, 886 for TEF1- α , and 1037 for RPB2). The resulting topology was similar for maximum likelihood (ML) and Bayesian analysis (Fig. 1). The analysis confirmed the placement of *Strigulales* with related orders in *Dothideomycetes* and the separation of the two families *Strigulaceae* and *Tenuitholiascaceae* (see Jiang et al. 2020). In this broad-scale analysis, foliicolous representatives of *Strigula* formed six clades (A–F) with strong support (between 95% and 100% BS and 100% PP).

For the *Strigulales* taxon set, with *Tenuitholiascus porinoides* S.H. Jiang, Lücking & J.C. Wei as outgroup, the concatenated alignment had the same length parameters. In the resulting topology (Fig. 2), the six clades of foliicolous *Strigula* s.lat. were again supported (between 82 and 100% BS and 100% PP), with the same topology. The six clades were composed as follows (Fig. 1): clade A included the type species, *S. smaragdula*, and corresponds to *Strigula* s.str.; clade B represented a newly recognized group of species with peculiar macroconidia (see below), for which the name *Serusiauxiella* is introduced below; clade C included two hypophyllous species with large ascospores centered around *Raciborskiella janeirensis* (Müll. Arg.)

R. Sant., and the name *Raciborskiella* is available for this clade; clade D featured species with non-carbonized perithecial wall, with the name *Puiggariella* available; clade E comprised the species of the *S. subtilissima* (Fée) Müll. Arg. aggregate, for which the name *Racoplaca* exists; and clade F contained the supracuticular species formerly separated in the genus *Phylloporis*. The non-foliicolous *Strigula jamesii* clustered in a separate clade, sister to foliicolous *Strigula* s.lat., together with *Flavobathelium* and *Phyllobathelium*.

The ITS-based tree for the genus *Serusiauxiella* (Fig. 3) revealed three species-level lineages, with two species being closely related on shallow stem branches and one species being phylogenetically quite distinct on a long stem branch. These are formally introduced below as *Ser. filifera* sp. nov., *Ser. flagellata* sp. nov., and *Ser. sinensis* sp. nov. The latter two are very closely related but differ in 18 substitutions and two indels in the ITS, for an overall similarity of 95.6%, distinctly below the standard species threshold level of 98.5% (Suppl. File S1). The rather shallow topology between these two species is therefore due to the substantial differences compared to *S. filifera* (95 substitutions, 26 indels; 73.5% similarity) and the outgroup taxon, *S. smaragdula*. This indicates an unusually high interspecific and intergeneric variation in the ITS, compared to notably uniformity within species, making the ITS barcoding marker an ideal locus to delimit species in foliicolous *Strigula* s.lat.

Table 5 Topology and position of major clades in foliicolous *Strigula* s.lat. in the four individual markers and the concatenated data set

Lineage	Feature	nuSSU	nuLSU	TEF1- α	<i>RPB2</i>	Concatenated
<i>Phylloporis</i>	Topology	Mono, LB (100%)	Mono, LB (100%)	Mono, LB (100%)	Mono, LB (100%)	Mono, LB (100%)
	Position	Sister to Rac + Ser + Str (unsupported)	Sister to Rac + Ser (96%)	Sister to outgroup (unsupported)	Sister to Str (90%)	Sister to all other lineages (97%)
<i>Puiggariella</i>	Topology	Mono, SB (100%)	Mono, LB (100%)	Mono, SB (87%)	mono, LB (100%)	Mono, SB (100%)
	Position	Sister to Rac (unsupported)	Sister to Rpl (92%)	Sister to Rpl (unsupported)	Sister to Ser (73%)	Sister to Rac + Ser (91%)
<i>Raciborskiella</i>	Topology	Mono, LB (100%)	Mono, LB (100%)	Mono, LB (100%)	[No data]	Mono, LB (100%)
	Position	Sister to Pui (unsupported)	Sister to Ser (94%)	Sister to Ser + Str (unsupported)	[No data]	Sister to Ser (98%)
<i>Racoplaca</i>	Topology	Mono, SB (100%)	Mono, LB (100%)	Mono, LB (100%)	Mono, LB (100%)	MONO, SB (100%)
	Position	Sister to <i>S. prasina</i> clade (89%); sister to Ser (unsupported)	Sister to Pui (92%)	Sister to Pui (unsupported)	Sister to Pui + Ser (unsupported)	SISTER to Pui + Rac + Ser (95%)
<i>Serusiauxiella</i>	Topology	Mono, LB (100%)	Mono, LB (100%)	Mono, LB (100%)	Mono, LB (100%)	Mono, LB (100%)
	Position	Sister to Rpl + <i>S. prasina</i> clade (unsupported)	Sister to Rac (94%)	Sister to Str core (70%)	Sister to Pui (73%)	Sister to Rac (98%)
<i>Strigula</i> s.str.	Topology	Mono, SB (100%) (except <i>S. prasina</i> clade)	Paraphyletic (unsupported)	Poly, SB (unsupported)	Mono, SB (98%)	Mono, SB (95%)
	Position	Sister to Rpl + Ser + <i>S. prasina</i> clade (80%)	MOSTLY basal to Phy + Rac + Ser; <i>S. prasina</i> and <i>S. nitidula</i> clades separate from core (unsupported)	Core sister to Ser (70%); <i>S. nitidula</i> and <i>S. prasina</i> clades sister to Pui + Rpl (78%)	Sister to Phy (90%)	Sister to Pui + Rac + Rpl + Ser (97%)

Supported conflict of individual markers with the concatenated data set is highlighted in boldface

Phy *Phylloporis* clade, Pui *Puiggariella* clade, Rac *Raciborskiella* clade, Rpl *Racoplaca* clade, Ser *Serusiauxiella* clade, Str *Strigula* s.str. clade

Morphology and anatomy of foliicolous *Strigula* s.lat

Specimens of *Strigula* s.lat. examined in this study are all characterized by a *Strigula*-type ascus apex, i.e. bitunicate, with a short tholus or ocular chamber at the tip, by which this clade can be distinguished from the sister group *Tenuitholiascaceae* (Jiang et al. 2020). As outlined above, the six foliicolous *Strigula* clades correlate with various phenotype characters, including photobiont type, thallus disposition, perithecial wall structure, ascospores, and macroconidida, particularly the nature of their appendages (Fig. 4).

Thallus morphology was found to be strongly correlated with phylogeny. Apart from the supracuticular species in clade F (*Phylloporis*), the subcuticular species in the remaining five clades exhibit four distinctive thallus types: clades A (*Strigula* s.str.) and B (*Serusiauxiella*) feature mostly thickened, bright green to grey-green thalli, whereas clade C (*Raciborskiella*) has very thin, bluish grey thalli composed of dispersed patches and clade E (*Racoplaca*) includes species with olive-brown to dark olive-green, somewhat metallic thalli forming delicate lobes delimited by thin black,

continuous or interrupted lines. Finally, clade D (*Puiggariella*) includes closely related species with a continuous to lobed, pale greenish thallus with somewhat folded surface and abundant white papillae.

The involucrellum of the perithecia is mostly carbonized to various degrees but consistently uncarbonized in clade D (*Puiggariella*). Ascospores show similar variation in most clades, ranging from small to medium-sized (less than 30 μm long) and in shape from oblong to fusiform. Exceptions are clade C (*Raciborskiella*), with large ascospores (30–70 μm long), and clade F (*Phylloporis*), with consistently small ascospores (up to 12 μm). The ascospores of *Raciborskiella* also display terminal gelatinous appendages. Likewise, macroconidial appendages vary from short to medium-sized in clade A, C, D, and E, whereas clade B (*Serusiauxiella*) is characterized by a peculiarity of its macroconidial appendages. To elucidate this, we examined appendage length for the various lineages. Apparently, fresh mounts of any of the species in *Strigula* s.lat. feature macroconidia with rather short appendages only (15–25 μm). Depending on the lineage, after a given time period, these appendages may grow

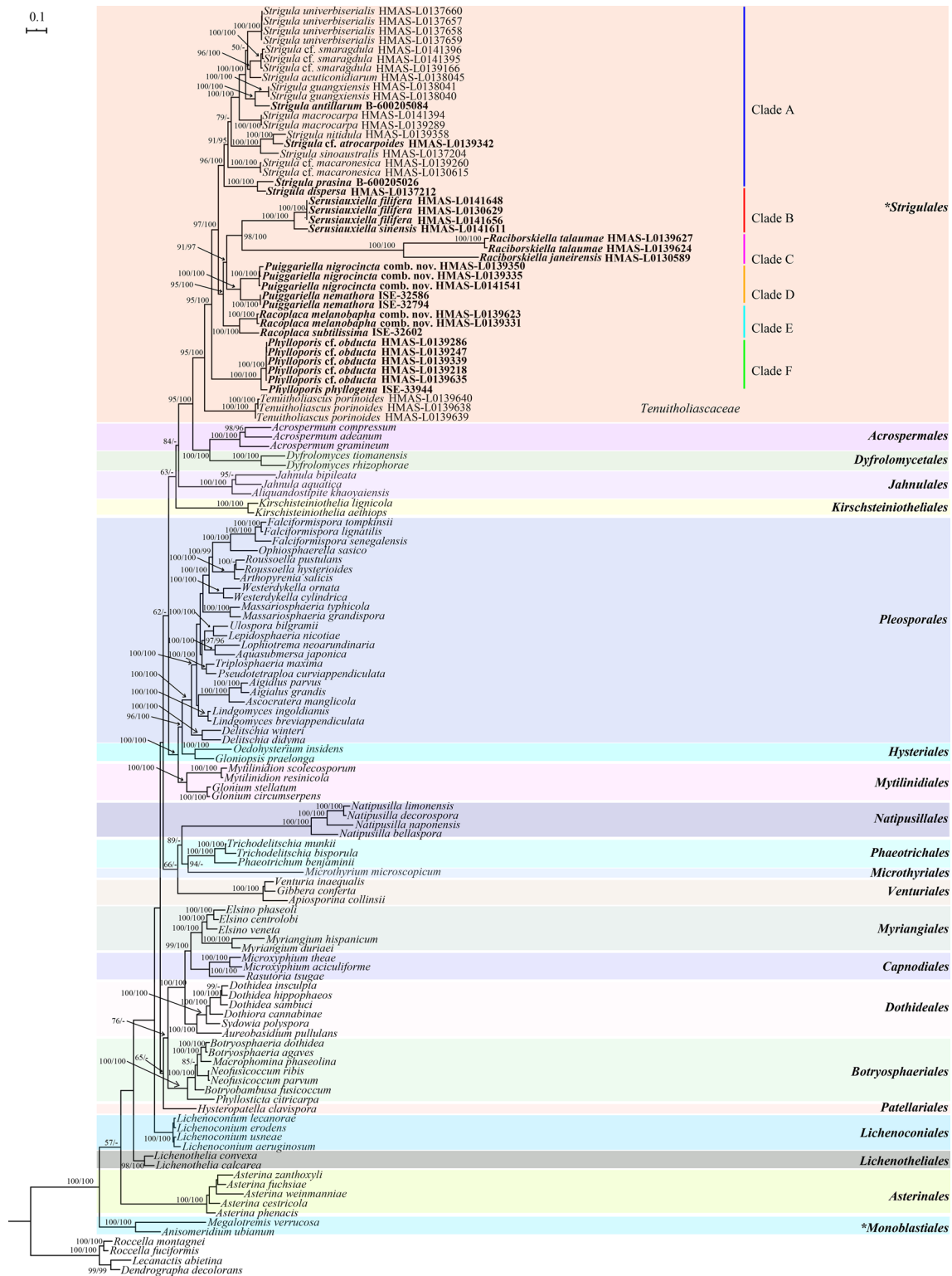


Fig. 1 Phylogenetic tree showing the delimitation of *Strigulales*, constructed through ML analysis in *Dothideomycetes* based on four marks (SSU, LSU, TEF1- α , and RPB2) with an alignment length of 4371 bp. Maximum likelihood bootstrap probabilities above 50%

(left) and Bayesian inference posterior probabilities above 90% (right) are shown at nodes (ML-BP/B-PP). Families and orders including lichenized taxa are marked with *. The tree was rooted with class *Arthoniomycetes*

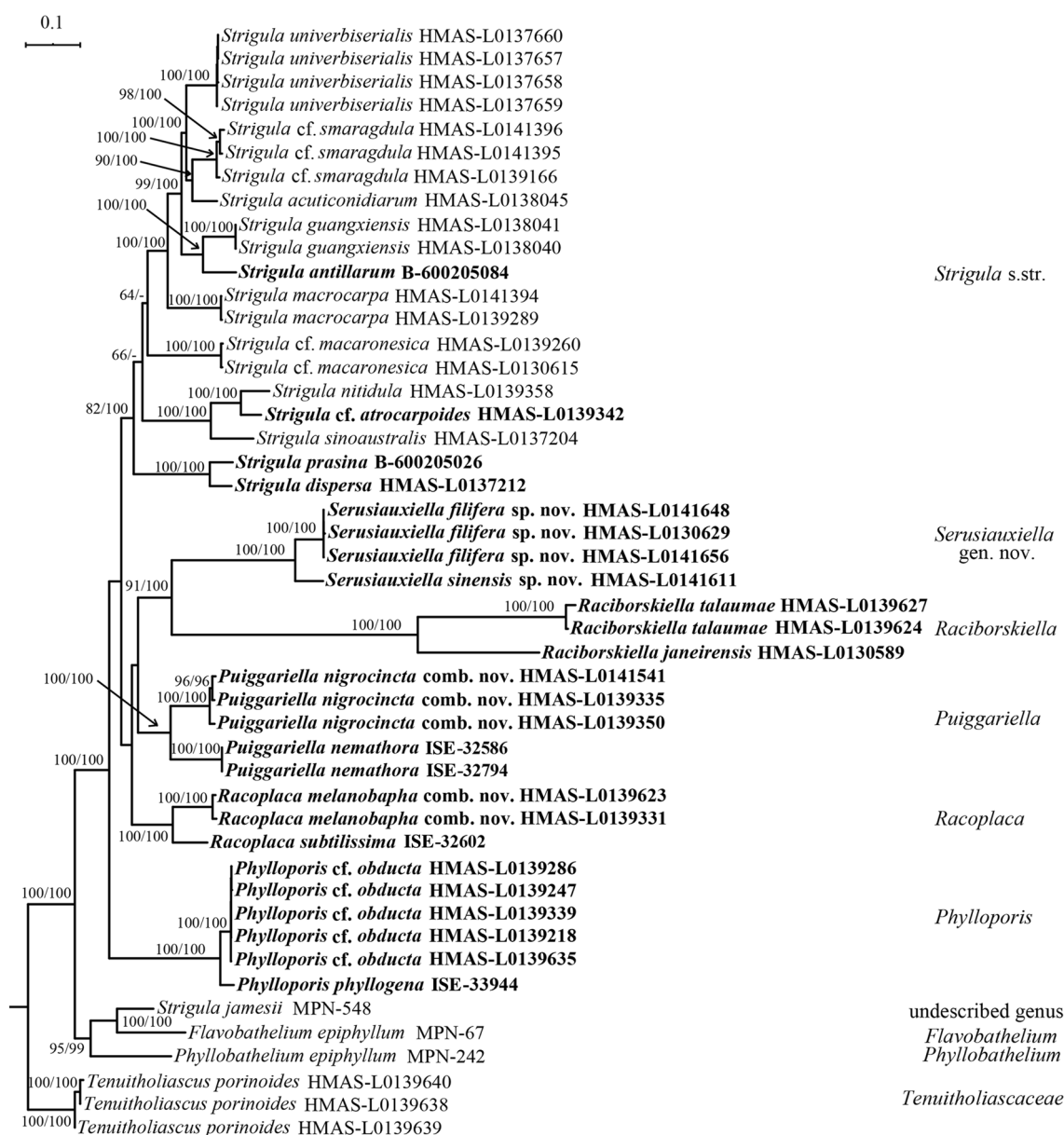


Fig. 2 Phylogenetic tree showing the internal phylogeny of *Strigulaceae*, constructed through ML analysis based on four markers (SSU, LSU, TEF1- α , and RPB2) with an alignment length of 4371 bp. Maximum likelihood bootstrap support above 50% (left)

and Bayesian inference posterior probabilities above 90% (right) are shown at nodes (ML–BP/B–PP). The tree was rooted with *Tenuitholiascus porinoides*

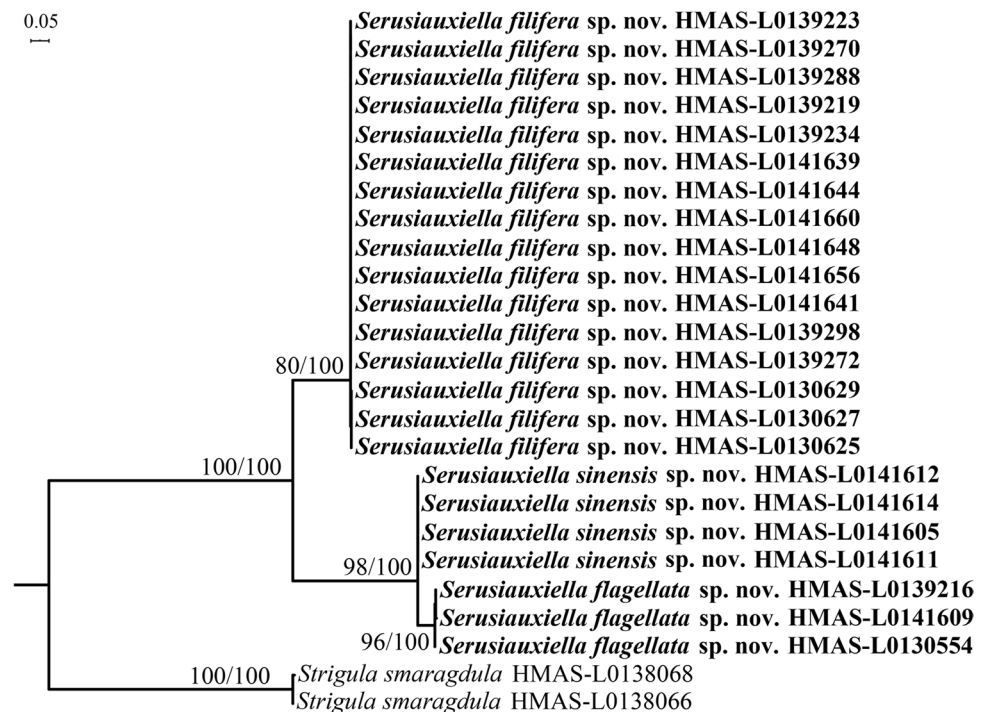
to considerable lengths. In all genera except *Serusiauxiella*, little change in appendage length was observed after 1 h, but after 1 day, appendages would often have extended to 50 μ m or more. In contrast, in all species of *Serusiauxiella*, the appendages extended to up to 70 μ m already after 1 h, much faster and to greater lengths than in the other genera. The functional role of this behaviour is unclear; since the appendages supposedly not contain plasma, they cannot be considered germ tubes, but their slow to rapid growth may have to do with fixation of the macroconidia on the

leaf surface. Notably, the ascospores do not exhibit such a behaviour.

Photobiont of selected foliicolous *Strigula* s.lat

Most foliicolous *Strigula* s.lat. clades (*Puiggariella*, *Raciborskiella*, *Racoplaca*, *Strigula*) feature a *Cephaleuros*-like photobiont (Fig. 5a), with anastomosing filaments or groups of cells usually arranged in one to several layers; these lichens grow subcuticularly and are not separable

Fig. 3 Phylogenetic tree showing species delimitation in *Serusiauxiella*, constructed through ML analysis based on ITS sequences with an alignment length of 447 bp. Maximum likelihood bootstrap probabilities above 50% (left) and Bayesian inference posterior probabilities above 90% (right) are shown at nodes (ML–BP/B–PP). The tree was rooted with *Strigula smaragdula*



from the leaf. The *Phylloporis* clade features *Phycopeltis* as photobiont, which anastomosing filaments in one layer and forming regular radiating plates or irregular nets (Fig. 5b); these lichens grow supracuticularly and can be easily separated from the leaf surface. A different, more *Trentepohlia*-like photobiont (Fig. 5c) was found in *Serusiauxiella*, which is remarkable as these species exhibit a similar thallus morphology and subcuticular growth as in *Strigula* s.str. Notably, thalli of *Serusiauxiella* can be removed from the leaf surface more easily than *Strigula* s.str. and the other subcuticular genera.

ITS sequence data confirmed our morpho-anatomical assessment of the photobionts, placing the photobionts of the studied lichens variously in proximity to lineages classified as *Cephaleuros*, *Phycopeltis*, or *Trentepohlia* (Fig. 6). However, these generic assignments are provisional, given that broader studies on trentepohlioid algae indicate that of the morphologically delimited genera within *Trentepohliaceae*, only *Cephaleuros* and *Stromatochroon* are monophyletic and the others (*Phycopeltis*, *Printzina*, *Trentepohlia*) are polyphyletic (Nelsen et al. 2011a; Zhu et al. 2017).

Assessment of non-foliicolous *Strigula* s.lat

The only non-foliicolous species of *Strigula* s.lat. sequenced thus far, *Strigula jamesii*, grows on rocks and is characterized by having 3-septate ascospores, with the

second cell often the widest and 3-septate macroconidia (Swinscow 1967; Roux and Sérusiaux 2004). This species does not cluster with the foliicolous taxa and the underlying topology suggests that non-foliicolous taxa do not represent *Strigula* s.str. or related foliicolous genera. No other generic name exists for these taxa and the name *Geisleria* cannot be used (see above). Given that non-foliicolous species may represent more than one entity (Roux and Sérusiaux 2004; Lücking et al. in Hyde et al. 2013), and only one species has been sequenced so far, we refrain from proposing a new genus for the single sequenced species here. The non-foliicolous species currently classified in *Strigula* s.lat. are being treated in a separate paper (Jiang et al., in prep.).

Discussion

Our analysis revealed the division of foliicolous *Strigula* s.lat. into six well-supported clades. Each clade is characterized by one or several unique synapomorphies. Clade A includes the type species *Strigula smaragdula* and is characterized by usually thickened, bright green to grey-green thalli with a *Cephaleuros* photobiont, with carbonized perithecial walls, small to medium-sized ascospores and short to medium-sized macroconidial appendages without rapid growth in microscopic mounts. Most foliicolous species of *Strigula* belong in this clade. Clade B is an entirely novel lineage recognized here, under the name

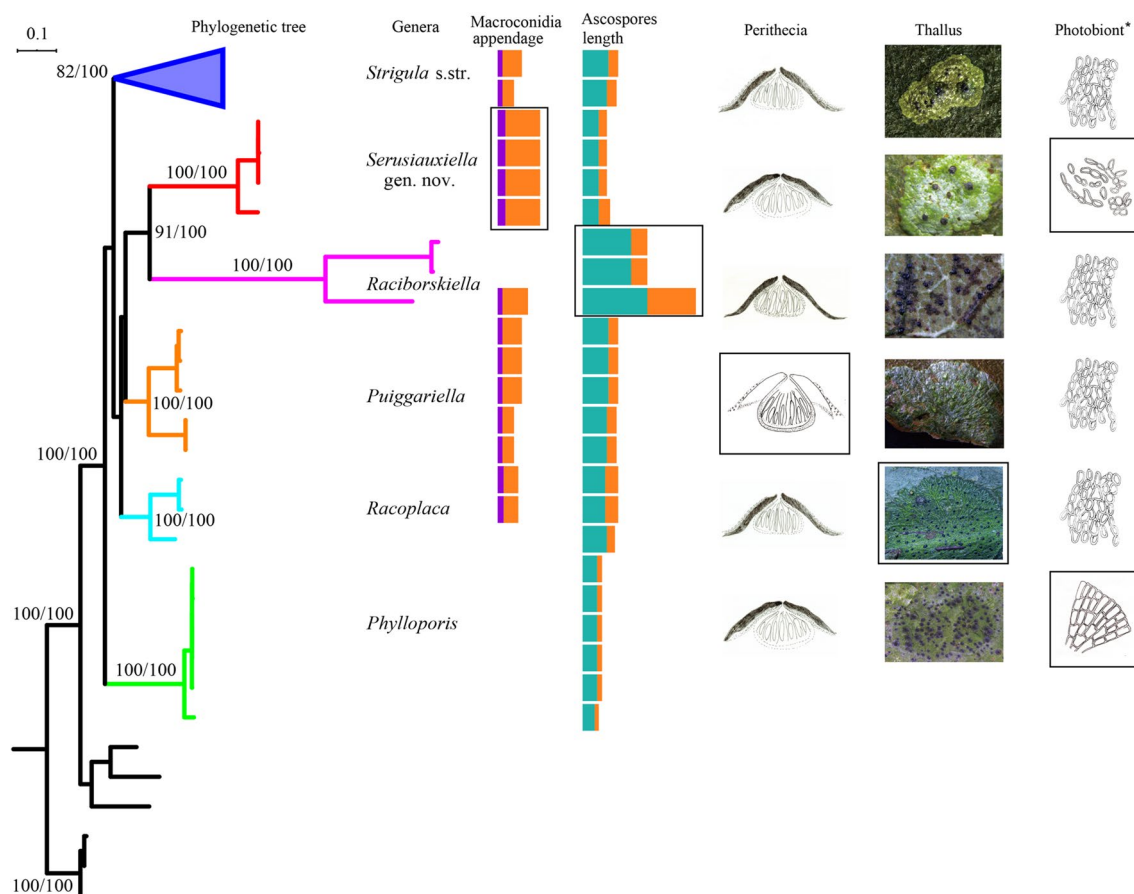


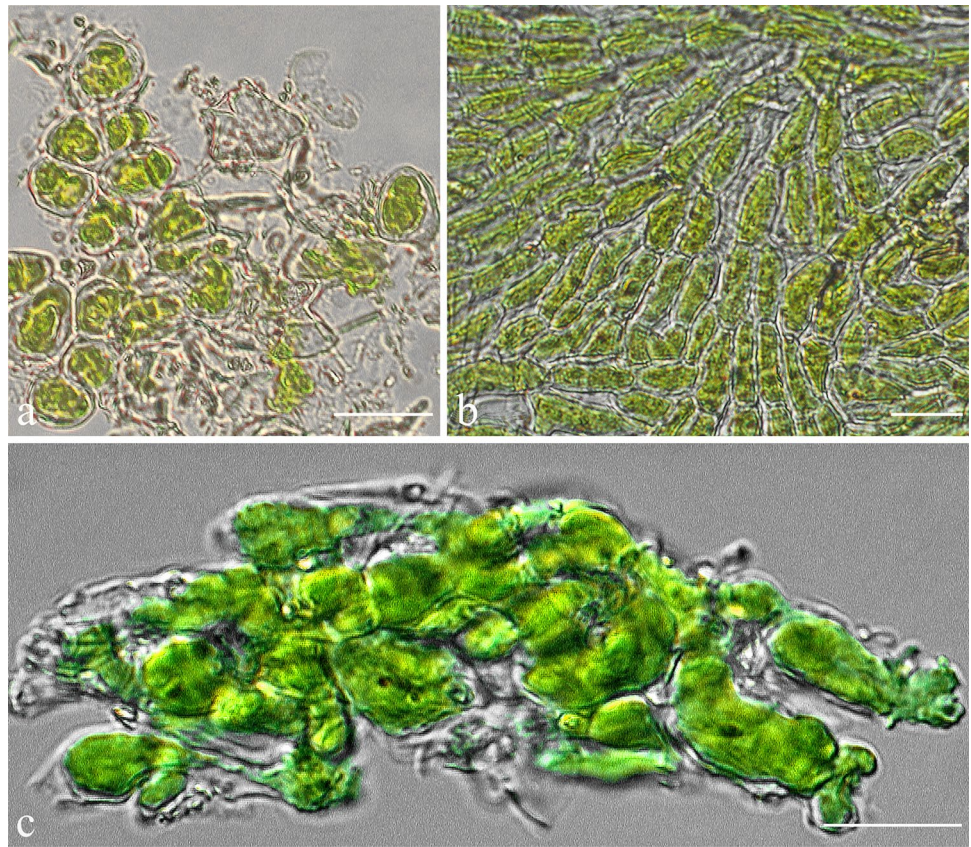
Fig. 4 Synoptic phylogenetic tree of *Strigulaceae* showing mapped phenotype features. The asterisk* indicates original photobiont drawings by Lücking (1992)

Serusiauxiella, on a very long stem branch, with three species new to science. The three species are morphologically rather uniform, resembling e.g. *Strigula microspora* Lücking in habit and ascospore size. However, the appendages of the macroconidia in this clade are unique, in microscopic mounts quickly growing to up to 70 μm and making the macroconidia appear as if suspended on long, gelatinous strands. In addition, the photobiont in this clade appears to be different from other subcuticular *Strigula* s.lat., clustering with *Trentepohlia* and also morphologically resembling that genus rather than *Cephaleuros*. Clade C includes two species previously classified under the name *Strigula janeirensis*, but representing two lineages separated by ascospore size (see below). Both agree in the hypophyllous growth, forming very thin, dark bluish grey thalli with *Cephaleuros* photobiont, carbonized perithecial walls, large ascospores (30–70 $\times$ 5–7 μm), with appendages at both ends (see also Roux and Sérusiaux 1995), and macroconidia with short to medium-sized appendages. In addition, the paraphyses in this clade are slightly branched and anastomosing (Santesson 1952). These differences were not accepted for generic delimitation and therefore *Raciborskiella* was subsumed

under *Strigula* (Harris 1975). However, this group is well-delimited both phylogenetically (longest branch in the tree) and phenotypically and hence the genus *Raciborskiella* is reinstated here. Another hypophyllous species previously included in *Raciborskiella*, *S. prasina* (Santesson 1952), has strongly deviating phenotype features fitting with *Strigula* s.str. (clade A) and is also included there phylogenetically.

Clade D is a small clade characterized chiefly by thallus morphology (with somewhat folded surface and abundant papillae) and pale, non-carbonized perithecial walls. The principal species in this clade, *S. nemathora*, is indeed quite distinct from all other foliicolous *Strigula* species, and our data suggest that it is a collective taxon, comprising several closely related species. The name *Puiggariella* is taken up for this genus. Clade E comprises the species of the *Strigula subtilissima* group, with thin, finely lobed thalli of olive-brown to dark (olive-)green color which feature a characteristic, thin black line along the lobe margins. Ascospores, macroconidia and other characters are otherwise similar to clade A (*Strigula* s.str.). The only superficially similar species in clade A is *S. nitidula*, which differs in the bright green thallus and the completely exposed, black perithecia,

Fig. 5 **a** *Cephaleuros* sp. from *Strigula smaragdula* (HMAS-L0138067), **b** *Phycopeltis* sp. from *Phylloporis* cf. *obducta* (HMAS-L0139237), **c** *Trentepohlia* sp. from *Serusiauxiella filifera*. (HMAS-L0130626). Scale bars: **a** = 20 μ m, **b**, **c** = 10 μ m



whereas those of the *S. subtilissima* group are covered by thallus up to the ostiole. We resurrect the name *Racoplaca* for this clade below. Clade F comprises the small *Strigula phyllogena* group, with thin, supracuticular thalli featuring a *Phycopeltis* photobiont, carbonized perithecial walls, and comparatively short asci and small ascospores. The genus *Phylloporis* was established for this group by Clements (1909), but the species were treated under *Porina* by Santeson (1952) and eventually included in *Strigula* by Harris (1995). Phylogenetically, the group is also quite distinctive. It is therefore justified to take up the genus *Phylloporis* for this clade.

Overall, all foliicolous lineages of *Strigula* s.lat. form a monophyletic clade, separate from the only non-foliicolous species currently placed in *Strigula*, *S. jamesii*. This indicates that most non-foliicolous species are not actually part of *Strigula* s.lat. but have to be redispositioned otherwise (Jiang et al., in prep.). For the foliicolous lineages, two alternatives exist to reflect the division into six clades taxonomically: (1) recognizing the six lineages at genus level or (2) separating them at subgeneric level. The phylogeny itself does not provide conclusive data to favor one or the other solution, although the long branches of three of the six lineages (*Phylloporis*, *Raciborskiella*, *Serusiauxiella*) indicate a substantial period of separate evolutionary history

that would justify generic status, which in turn would then require to also recognize the other three lineages as separate genera.

The concept of the so-called “evolutionary significant unit” (ESU), in tandem with the notion that the binomial offers the inclusion of phylogenetic affinities, provides another approach to solve this matter. Originally, the term was coined to denote species- or population-level lineages that due to unique genetic makeup deserve conservation status (Moritz 1994; Casacci et al. 2014; Cornejo et al. 2017). However, the concept can be expanded to genus-level taxonomy, with the argument that ESUs above species level should be reflected in their nomenclature. The standard nomenclature for species is the binomial, including the name of the genus and the specific epithet. Infrageneric subdivisions are not reflected in the binomial and there are not established standard citation forms of infrageneric classifications in botanical or mycological nomenclature, in contrast to zoological nomenclature. Therefore, if the six lineages above would be recognized at infrageneric level (e.g. as subgenera), standard listings or name citations would not reflect this classification, as the species would continue to be listed and cited under the genus *Strigula*. Since these lineages strongly correlate with phenotype features and are “recognizable” as taxonomic units, we consider them

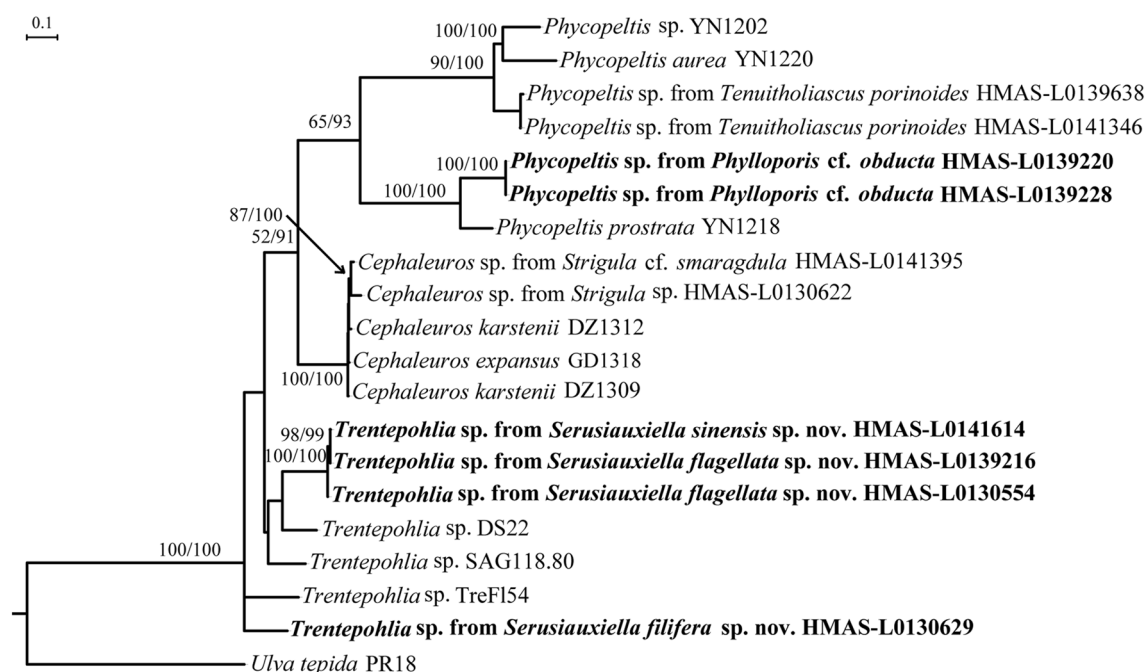


Fig. 6 Phylogenetic tree of selected *Trentepohliaceae*, constructed through ML analysis based on ITS. Maximum likelihood bootstrap support above 50% (left) and Bayesian inference posterior probability above 90% (right) are shown at nodes (ML–BP/B–PP). The new sequences generated in this study are indicated in boldface

to represent ESUs above species level and the only way to recognize this properly in their nomenclature is to establish generic rank for each lineage. We therefore introduce a revised generic concept below for foliicolous representatives of *Strigula* s.lat.

Taxonomic treatment

Key to genera of *Strigulaceae* containing foliicolous species

In the key below, genera not explicitly treated in this study are given in brackets; the remaining genera are treated in the order of the phylogeny (Fig. 1).

1. Ascospores transversely septate..... 2
1. Ascospores muriform..... 8
2. Perithecia immersed in thalline verrucae, aggregated in pseudostromata filled with ochraceous-yellow, K + red crystals; paraphyses rather thick (1.5–2 μ m); pycnidia aggregate in pseudostromata similar to those of perithecia; macroconidia acicular, 3–5-septate, one end with gelatinous appendages, the other with gelatinous cap..... [*Flavobathelium*]
2. Perithecia exposed or covered by thallus layer, solitary or clustered but not in pseudostromata; pycnidia soli-

- tary or aggregate but not in pseudostromata filled with ochraceous-yellow crystals3
3. Perithecial wall not carbonized; thallus subcuticular, with numerous minute, white papillae **4. *Puiggariella***
3. Perithecia carbonized; thallus variable, very rarely with white papillae4
4. Thallus supracuticular, easily separated from the leaf surface; photobiont *Phycopeltis* (forming radiating or reticulate plates of rectangular cells)**6. *Phylloporis***
4. Thallus subcuticular, more difficult to separate from the leaf surface; photobiont *Cephaleuros* or *Trentepohlia* (forming one or several layers of irregular groups or threads of angular-rounded cells)5
5. Ascospores large (30–70 μ m long); thallus thin, typically dark bluish grey, always hypophyllous..... **3. *Raciborskiella***
5. Ascospores small to medium-sized (7–25 μ m); thallus thin to thickened, usually bright to dark green to grey-green or olive-brown, usually epiphyllous, rarely bluish grey and/or hypophyllous6
6. Thallus olive-brown to dark green, with a somewhat metallic shine, composed of dichotomously branched lacinia bordered by a continuous or interrupted black line; perithecia covered by thin thallus layer up to ostiole, therefore not pure black**5. *Racoplaca***
6. Thallus bright green to grey-green or rarely with bluish tinge, with entire to crenulate or lobed margin but

- rarely lacinate, not bordered by a thin black line except in the *S. nitidula* aggregate and then thallus green and perithecia exposed, black..... 7
7. Macroconidia with appendages quickly elongating (up to 70 µm) after waiting up to 1 h in squash mounts, often appearing as if suspended along gelatinous strands; photobiont *Trentepohlia*..... **2. *Serusiauxiella***
7. Macroconidia with appendages remaining short to medium-sized (usually up to 30 µm) after 1 h in squash mounts, becoming longer only after long periods of time (1 day); photobiont *Cephaleuros*..... **1. *Strigula s.str.***
8. Perithecia immersed in thalline verrucae usually filled with black, pulveraceous crystals; pycnidia usually aggregate in pseudostromata, rarely solitary in thalline verrucae..... [*Phyllobathelium*]
8. Perithecia exposed or covered by very thin thallus layer, not immersed in thalline verrucae; pycnidia usually solitary and partly exposed..... [*Phyllocratera*]

1. *Strigula* Fr., Syst. Mycol. (Lundae) 2(2): 535 (1823).

Mycobank: MB 5285

Type: *Strigula smaragdula* Fr.

Notes: This more narrowly defined genus is characterized by a foliicolous growth habit forming subcuticular thalli with a *Cephaleuros* photobiont. The thalli are typically thickened, mostly bright green to grey-green. The perithecial wall is invariably carbonized and appears jet-black in sections. Ascospores are uniseriate to biseriate in the asci, 1-septate (very rarely 3-septate) and small to medium-sized (7–25 × 4–6 µm). The appendages of the macroconidia are short to medium-sized and extend only slowly in squash mounts. Most foliicolous species currently placed in *Strigula* s.lat. belong here, except those outlined below under the newly recognized genera.

***Strigula smaragdula* Fr., Linnaea 5: 550 (1830).**

Fig. 7

Mycobank: MB 431363

Type: Nepal. Unknown locality; on leaves of *Loranthus ligustroides*; König s.n. (lectotype, UPS!; Santesson 1952: 160, as “holotype”).

Notes: In its current taxonomic concept, *Strigula smaragdula* is characterized by bright green, thickened thallus patches, basally immersed and apically erumpent perithecia partly covered by a thallus layer and with a diffuse limit between the thallus and involucrellum, fusiform, 1-septate ascospores 15–25 × 4–6 µm in size, and bacillar, 1-septate macroconidia 12–20 × 3–4 µm (Fig. 7). Several other species are similar: *S. macrocarpa* Vain. has a thinner thallus and larger, prominent perithecia; *S. nigrocarpa* Lücking has exposed, black perithecia sharply contrasting with the thallus, and *S. subelegans* Vain. has a bluish grey thallus. *Strigula smaragdula* is likely a collective taxon (Woo et al. 2020).

The original material is from Nepal and India; Santesson (1952) only cited the material from Nepal, as “holotype”, but technically it constitutes a lectotypification (ICN Art. 9.10), which means that the bulk of tropical material may not represent that species.

Distribution and ecology: *Strigula smaragdula* in its current circumscription is presumed to be pantropical (Santesson 1952; Lücking 2008). However, molecular studies indicate that it might deal with a collective taxon (Jiang et al. 2017a; Woo et al. 2020). For instance, the European material is now being recognized as separate species, *S. buxi* (Roux and Sérusiaux 2004). Numerous synonyms exist to potentially cover segregate species in various geographic regions (Santesson 1952; Lücking 2008). For the time being we can only confirm the presence of *S. smaragdula* in continental Asia, in accordance with the origin of the type material. From China, it was reported from five provinces (Fujian, Guizhou, Hubei, Hunan, Yunnan) by Santesson (1952). Examination on new material extends the Chinese range to Guangdong, Guangxi, Hainan, Hongkong, and Xizang provinces.

Specimens examined: CHINA. Guangdong: Shixing County, Chebaling National Nature Reserve; 24° 42' 35" N, 114° 13' 37" E, 398 m; on living leaves; 14 May 2015, X.L. Wei & J.H. Wang GD2015031_5 (HMAS-L0139166); *ibid.*; 345 m; on living leaves; 14 May 2015, X.L. Wei & J.H. Wang GD2015025_5 (HMAS-L0138067); *ibid.*; 24° 42' 39" N, 114° 13' 30" E, 387 m; on living leaves, 15 May 2015, X.L. Wei & J.H. Wang GD2015038_22 (HMAS-L0139171); *ibid.*; 24° 44' 07" N, 114° 12' 31" E, 486 m; on living leaves, GD2015042_12 (HMAS-L0138068), GD2015042_12_3 (HMAS-L0141591). Guangxi: Nanning City, Long'an County, Longhu Mountain Natural Reserve; 22° 57' 42" N, 107° 37' 40" E, 147 m, on living leaves; 1 December 2015, S.H. Jiang GX201511165 (HMAS-L0139279), GX201511084 (HMAS-L0138050). Yulin City, Beiliu County, Darongshan Nature Reserve; 22° 51' 46" N, 110° 16' 31" E, 495 m, on living leaves of shrubs; 7 December 2015, S.H. Jiang GX201511037 (HMAS-L0139265), GX201511039 (HMAS-L0139266), GX201511042_2 (HMAS-L0141638), GX201511042 (HMAS-L0139267), GX201511031 (HMAS-L0139264); *ibid.*; 460 m; 15 December 2016, X.Q. Zhang GX2016001 (HMAS-L0139215), GX2016001_2 (HMAS-L0141630), GX2016002 (HMAS-L0139214), GX2016003 (HMAS-L0139213), GX2016004 (HMAS-L0139212), GX2016004_2 (HMAS-L0141631), GX2016005 (HMAS-L0139211), GX2016005_2 (HMAS-L0141632), GX2016005_3 (HMAS-L0141633), GX2016005_4 (HMAS-L0141636), GX2016005_5 (HMAS-L0141637), GX2016006 (HMAS-L0139209), GX2016006_2 (HMAS-L0141634), GX2016006_3 (HMAS-L0141635), GX2016007 (HMAS-L0139210). Shangsi County, Shiwan

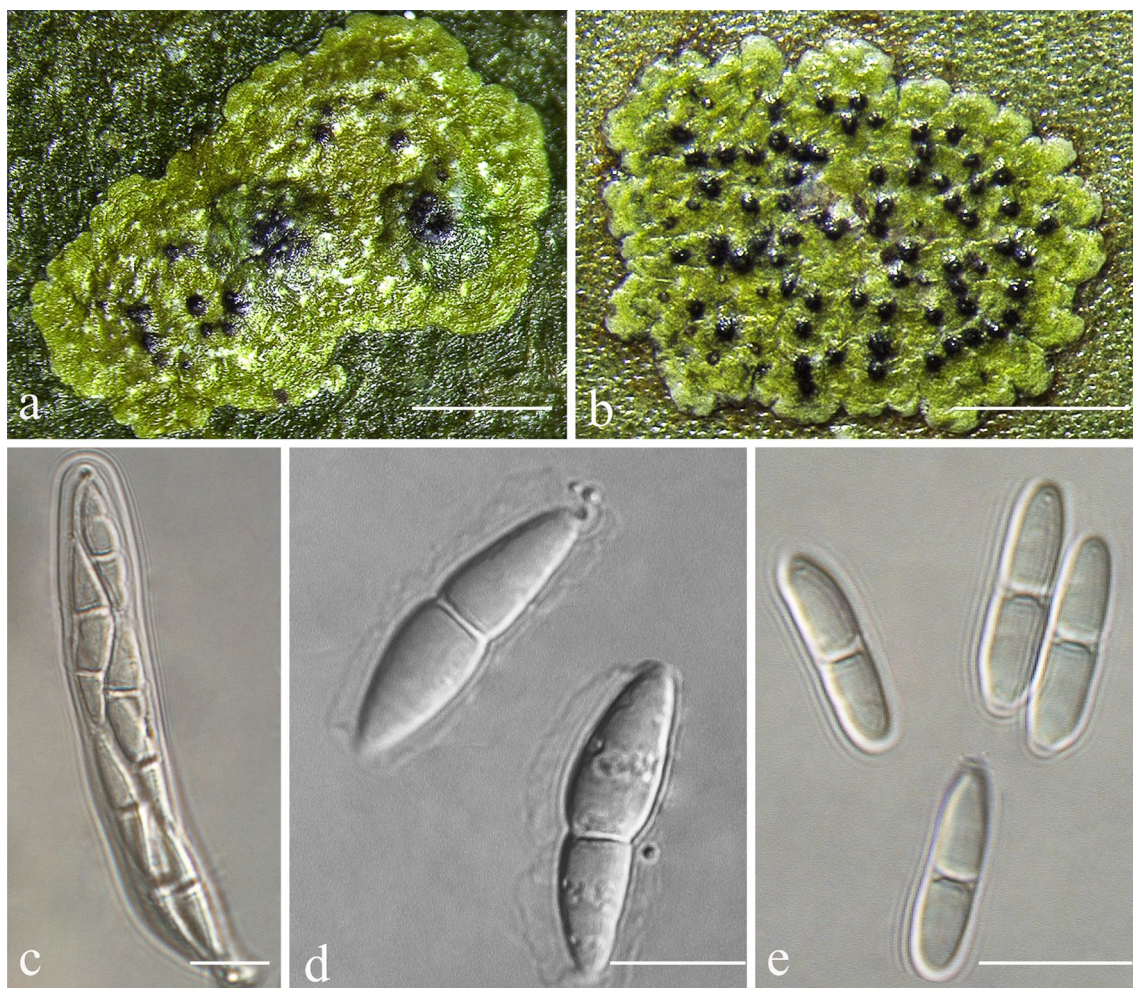


Fig. 7 *Strigula smaragdula* **a** Thallus with perithecia (HMAS-L0138067), **b** Thallus with pycnidia (HMAS-L0130621), **c** Ascus (HMAS-L0138066), **d** Ascospores (HMAS-L0138066) **e** Macroconidia (HMAS-L0138066). Scale bars: **a, b** = 300 µm, **c–e** = 10 µm

Mountain National Natural Reserve; 21° 54' 13" N, 107° 54' 13" E, 264 m; on living leaves; 5 December 2015, S.H. Jiang GX201511378 (HMAS-L0139294), GX201511378_3 (HMAS-L0141667). Longzhou County, Nonggang National Nature Reserve; 22° 27' 55" N, 106° 57' 5" E, 270 m; on living leaves; 3 December 2015, S.H. Jiang, GX201511211 (HMAS-L0139316); *ibid.*; 268 m; 24 May 2015, X.L. Wei & J.H. Wang GX20150197 (HMAS-L0139273); *ibid.*; 22° 29' 15" N, 106° 56' 45" E, 268 m; 24 May 2015, X.L. Wei & J.H. Wang GX20150188 (HMAS-L0139271); *ibid.*; 200 m, 23 May 2015, X.L. Wei & J.H. Wang GX20150134 (HMAS-L0138066), GX20150137_4 (HMAS-L0141391), GX20150143 (HMAS-L0139269); *ibid.*; 22° 28' 11" N, 106° 57' 21" E, 200 m; 23 May 2015, X.L. Wei & J.H. Wang GX20150131_3 (HMAS-L0141578). Hainan, Dongfang City, Yalong village; 18° 59' 2" N, 108° 53' 22" E, 191 m; on living leaves; 14 December 2014, X.L. Wei & S.H. Jiang HN2014441_4 (HMAS-L0141624), HN2014441_5 (HMAS-L0141624), HN2014330 (HMAS-L0130621),

HN2014330_3 (HMAS-L0141621), HN2014330_4 (HMAS-L0141622), HN2014330_2 (HMAS-L0141395). Hongkong: Xinjie North District; 159 m; on living leaves; 9 December 2011, J.C. Wei & W. Guo HK126 (HMAS-L0139393), HKG-3 (HMAS-L0139394). Xizang: Motuo County, Dexing village; 29° 42' 48" N, 95° 36' 43" E, 870 m; on living leaves; 9 September 2014, X.L. Wei & Y.Y. Wang XZ20140521 (HMAS-L0139392), XZ20140526 (HMAS-L0139398), XZ20140527 (HMAS-L0139397). Yunnan: Pu'er City, Simao District S214; 1316 m; on living leaves; 23 October 2016, X.Y. Liu YN20160044 (HMAS-L0139175). Xishuangbanna, Jinghong City; 22° 19' 15" N, 100° 47' 13" E, 968 m; on living leaves; 28 October 2016, X.Y. Liu YN20160092 (HMAS-L0139195), YN20160096 (HMAS-L0139190). Mengla County; 21° 36' 5" N, 101° 34' 36" E, 678 m; on living leaves; 24 October 2016, X.Y. Liu YN20160058 (HMAS-L0139182).

2. *Serusiauxiella* S.H. Jiang, Lücking & J.C. Wei, **gen. nov.**

MycoBank: MB 833565

Type species: *Serusiauxiella filifera* S.H. Jiang, Lücking & J.C. Wei.

Diagnosis: Differing from *Strigula* s.str. in the *Trentepohlia* photobiont and the macroconidial appendages quickly growing to substantial length (up to 70–100 µm) in squash mounts.

Etymology: It is with great pleasure that we dedicate this new genus to Dr. Emmanuël Sérusiaux, in recognition of his important contributions to lichenology, foliicolous lichens and the genus *Strigula*.

Description: Thallus foliicolous, crustose, forming circular patches with entire to crenulate margins, grey-green, subcuticular but more or less separable from the leaf surface. Photobiont *Trentepohlia*. Perithecia immersed-erumpent, hemispherical to wart-shaped; excipulum prosoplectenchymatous, colorless; involucrellum mostly carbonized, black; hamathecium colorless, I–, KI–; paraphyses unbranched or rarely sparsely branched, thin. Asci bitunicate, with short tholus and narrow, ocular chamber, I–, KI–, clavate to oblong. Ascospores 8 per ascus, biseriate or irregularly arranged, fusiform, 1-septate, colorless, 7–15 × 2–5 µm. Pycnidia immersed-erumpent, wart-shaped, black. Macroconidia bacillar to filiform, 1-septate, colorless, both ends with gelatinous appendages that grow to up to 70 µm (sometimes up to 100 µm) in squash mounts after short time (1 h). Microconidia fusiform-ellipsoid, non-septate, colorless.

Chemistry: No substances detected by TLC.

Notes: As outlined above, the species of this new genus superficially resemble *Strigula* s.str., in particular *S. microspora* and similar taxa. Its most distinctive features are the macroconidial appendages becoming extremely long and the photobiont morphologically and phylogenetically representing a species of *Trentepohlia* rather than *Cephaleuros*. Thus far the genus includes three species, all new to science and so far only known from (sub-)tropical Asia.

Key to species of *Serusiauxiella*

1. Perithecia applanately hemispherical, erumpent and mostly covered by thallus, the exposed black ostiolar area up to 0.2 mm diam.; involucrellum distinctive in upper part, laterally fusing with thallus; ascospores with slightly tapering, rounded ends.....*Serusiauxiella filifera*
1. Perithecia hemispherical to wart-shaped or almost conical, prominent, the mostly exposed black portion up to 0.4 mm diam.; involucrellum confluent with excipulum in upper part; ascospores with strongly tapering, rounded to subacute ends2
2. Asci 50–80 µm long*Serusiauxiella flagellata*
2. Asci 40–65 µm long*Serusiauxiella sinensis*

Serusiauxiella filifera S.H. Jiang, Lücking & J.C. Wei, **sp. nov.** Fig. 8

MycoBank: MB 833566

Type: CHINA. Hainan: Dongfang City, Nanlang village E'xian Ling; 19°00'18" N, 109°04'09" E, 160 m; on living leaves; 13 December 2014, J.H. Wang & R.D. Liu HN2014362 (HMAS-L0130626).

Diagnosis: Characterized by its applanately hemispherical perithecia that are covered by thallus except for the uppermost portion, and by rather short asci.

Etymology: The epithet refers to the macroconidial appendages becoming long and filiform in squash mounts.

Description: Thallus epiphyllous, subcuticular, 2–8 mm across and 12–20 µm thick, sometimes growing along the nerves, margins, and scars of leaves, circular, with entire to crenulate or lobulate margins, bright green, but often becoming whitish in the center, different color shades often arranged in concentric zones, rather easily separated from leaf. Photobiont a species of *Trentepohlia*, cells angular-rounded, 5–10 × 3–6 µm. Perithecia usually present and abundant, immersed-erumpent, applanately hemispherical, 105–120 µm high; excipulum prosoplectenchymatous, 12–20 µm thick, colorless to blackish brown; involucrellum developed only in upper part, carbonaceous, laterally fusing with thallus, 30–45 µm thick; paraphyses unbranched or sparingly branched. Asci oblong, 37–53 × 10–12 µm. Ascospores biseriate or irregularly arranged, 8 per ascus, fusiform-ellipsoid, with more or less rounded ends, 1-septate, usually with 1–2 guttules in each cell when fresh and thus appearing 3-septate, especially in 10% KOH, slightly constricted at the septum, usually with the distal cell somewhat enlarged, not breaking into pieces, surrounded by a thin mucilaginous sheath, 10–15 × 2.5–5 µm. Pycnidia producing macroconidia 0.05–0.15 mm, immersed-erumpent, wart-shaped, black. Macroconidia bacillar, 1-septate, 12.5–15 × 2–3.5 µm, with gelatinous appendage at both ends, 13–25 µm long but in squash mounts quickly growing to 70 µm or more. Pycnidia producing microconidia not seen.

Chemistry: No substances detected by TLC.

Ecology and distribution: The new species grows on leaves in wet tropical forest in southern China. At present, it is known only from the type locality, but documented by numerous specimens.

Notes: This new species externally resembles *Strigula microspora* (Lücking 2008), from which differs chiefly by its rather applanate perithecia, short asci and biseriate ascospores. *Strigula caerulensis* P.M. McCarthy and *S. macaronesica* Sérus. also bear some resemblance, but in *S. caerulensis* the thallus is supracuticular, dull, and perithecia are rounded to subacute (McCarthy 2009b). *Strigula macaronesica* differs in its long linear thallus and larger ascospores (Sérusiaux 1997).

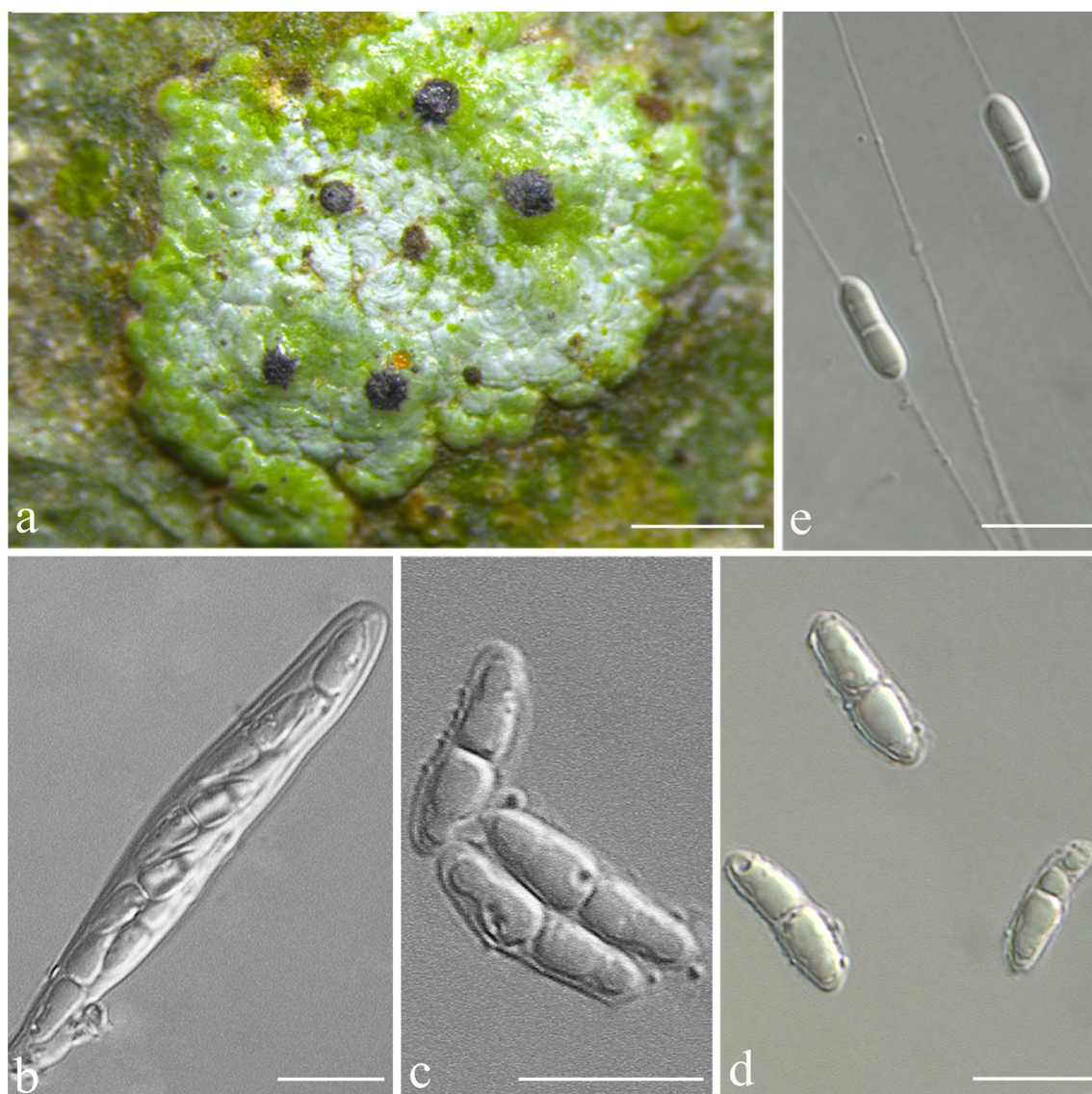


Fig. 8 *Seriauxiella filifera* sp. nov. (holotype, HMAS-L0130626) **a** Thallus, **b** Asci, **c**, **d** Ascospores, **e** Macroconidia with extremely long appendages. Scale bars: **a** = 600 μ m, **b–e** = 10 μ m

Additional specimens examined. CHINA. Guangxi: Nanning, Long'an County, Longhu Mountain Natural Reserve; 22° 57' 42" N, 107° 37' 40" E, 147 m; on living leaves; 1 December 2015, S.H. Jiang GX201511072_1 (HMAS-L0141639), GX201511074_2 (HMAS-L0141640), GX201511075 (HMAS-L0139297), GX201511079 (HMAS-L0139298), GX201511081_1 (HMAS-L0141641), GX201511082_1 (HMAS-L0141642), GX201511083_1 (HMAS-L0141643), GX201511086_1 (HMAS-L0141644), GX201511088_2 (HMAS-L0141645), GX201511093 (HMAS-L0139307), GX201511096 (HMAS-L0139308), GX201511096_2 (HMAS-L0141646), GX201511097 (HMAS-L0139309), GX201511098_1 (HMAS-L0141648), GX201511107 (HMAS-L0138043), GX201511133

(HMAS-L0139311), GX201511149 (HMAS-L0139313), GX201511153 (HMAS-L0139315). Longzhou County, Nonggang National Nature Reserve; 22° 27' 55" N, 106° 57' 5" E, 270 m; on living leaves; 3 December 2015, S.H. Jiang, GX201511199 (HMAS-L0139219), GX201511199_2 (HMAS-L0141651), GX201511209 (HMAS-L0139223), GX201511209_2 (HMAS-L0141652), GX201511210_2 (HMAS-L0141653), GX201511225 (HMAS-L0139288), GX201511227 (HMAS-L0139290), GX201511250_2 (HMAS-L0141655), GX201511259 (HMAS-L0139234), GX201511265_1 (HMAS-L0141656), GX201511265_2 (HMAS-L0141657), GX201511282_1 (HMAS-L0141660), GX201511281_3 (HMAS-L0141659), GX201511283 (HMAS-L0139323), GX201511317_2 (HMAS-L0141666),

GX201511319 (HMAS-L0139325); *ibid.*, 22° 59' 15" N, 106° 56' 45" E, 268 m; on living leaves; 24 May 2015, X.L. Wei & J.H. Wang GX20150187 (HMAS-L0139270), GX20150193 (HMAS-L0139272), GX20150193_2 (HMAS-L0141579). Hainan, Dongfang City, Nanlang village E' xian Ling; 19° 00' 18" N, 109° 04' 09" E, 160 m; on living leaves; 13 December 2014, J.H. Wang & R.D. Liu HN2014358 (HMAS-L0130625), HN2014373 (HMAS-L0130627), HN2014375 (HMAS-L0130629).

Serusiauxiella flagellata S.H. Jiang, Lücking & J.C. Wei, *sp. nov.* Fig. 9

Mycobank: MB 833568

Type: CHINA. Hainan: Ledong County, Jianfengling; 18° 44' 36" N, 108° 50' 39" E, 962 m; on living leaves; 12 December 2014, J.H. Wang & R.D. Liu HN20144632 (HMAS-L0139216).

Diagnosis: This species is most closely related to *Ser. sinensis*, from which it differs by its longer asci and in the following positions in the ITS (Suppl. File S1): [substitutions] A-G (143), C-T (49, 79, 81, 99, 124, 308, 316, 318, 361), G-C (314), T-C (17, 78, 87, 92, 105, 349); [indels] (80, 135).

Etymology: The epithet refers to the macroconidial appendages resembling flagellae.

Description: Thallus epiphyllous, subcuticular, 3–10 mm across and 15–30 µm thick, generally growing along the nerves, margins, and scars of leaves, circular, with entire to crenulate or lobulate margins, bright green, often becoming pale bluish-grey to whitish in the center. Photobiont a species of *Trentepohlia*, cells angular-rounded, 5–10 × 3–6 µm. Perithecia hemispherical to wart-shaped, basally immersed but for the most part exposed, 0.3–0.4 mm diam. and 80–170 µm high; excipulum prosoplectenchymatous, 5–10 µm thick, colorless to blackish brown; involucrellum carbonized, 10–20 µm thick, black; paraphyses unbranched or sparingly branched. Asci oblong, 50–80 × 7–10 µm. Ascospores biseri-ate, 8 per ascus, fusiform, with tapering, rounded to subacute ends, 1-septate, usually with 1–2 guttules in each cell, not breaking into pieces, surrounded by a thin mucilaginous sheath, 12–18 × 3–5 µm. Pycnidia producing macroconidia immersed-erumpent, wart-shaped, 0.1–0.15 mm, black. Macroconidia bacillar, 1-septate, 10–13 × 2.5–3.7 µm, with gelatinous appendages at both ends, 13–25 µm long but in squash mounts quickly growing to 70 µm or more. Pycnidia producing microconidia not seen.

Chemistry: No substances detected by TLC.

Ecology and distribution: *Serusiauxiella flagellata* is known through a number of collections from around the type locality in South China. It grows on leaves in wet tropic forest.

Notes: *Serusiauxiella flagellata* differs from *Ser. filifera* in the distinctly more exposed, hemispherical to wart-shaped

perithecia and the ascospores with more distinctly tapering ends. Phylogenetically, the two species differ in numerous substitutions in the ITS (see above).

Additional specimens examined: CHINA. Hainan: Ledong County, Jianfengling; 18° 44' 36" N, 108° 50' 39" E, 962 m; on living leaves; 12 December 2014, J.H. Wang & R.D. Liu HN2014240_4 (HMAS-L0141609); *ibid.*; 18° 44' 5" N, 108° 52' 8" E, 920 m; on living leaves; 11 December 2014, J.H. Wang & R.D. Liu HN2014131 (HMAS-L0130554).

Serusiauxiella sinensis S.H. Jiang, Lücking & J.C. Wei, *sp. nov.* Fig. 10

Mycobank: MB 833570

Type: CHINA. Hainan: Ledong County, Jianfengling, Mingfenggu; 18° 44' 32" N, 108° 50' 32" E, 985 m; on living leaves; 12 December 2014, J.H. Wang & R.D. Liu HN2014281_2 (HMAS-L0141614).

Diagnosis: Differing from *Serusiauxiella flagellata* chiefly in its shorter asci and in the following positions in the ITS (Suppl. File S1): [substitutions] C-G (314), C-T (17, 78, 87, 92, 105, 349), G-A (143), T-C (49, 79, 81, 99, 124, 308, 316, 318, 361), [indels] (80, 135).

Etymology: The epithet refers to the discovery of this new species in China.

Description: Thallus epiphyllous, subcuticular, 3–10 mm across and 10–20 µm thick, typically growing along the nerves, margins, and scars of leaves, circular, with entire to crenulate or lobulate margins, bright green but sometimes becoming whitish in the center. Photobiont a species of *Trentepohlia*, cells angular-rounded, 5–10 × 3–6 µm. Perithecia mostly erumpent, hemispherical to wart-shaped, 0.2–0.3 mm diam. and 100–180 µm high, exposed part black; excipulum prosoplectenchymatous, 5–10 µm thick, colorless to blackish brown; involucrellum carbonized, 10–30 µm thick, black; paraphyses unbranched or sparingly branched. Asci oblong, 40–65 × 5–10 µm. Ascospores biseri-ate or irregularly arranged, 8 per ascus, fusiform, with tapering, rounded to subacute ends, 1-septate, slightly constricted at the septum, not breaking into pieces, surrounded by a thin mucilaginous sheath, 10–18 × 3.5–5 µm. Pycnidia immersed-erumpent, wart-shaped, those producing macroconidia 0.1–0.15 mm, those producing microconidia 0.05–0.1 mm diam., black. Macroconidia bacillar, 1-septate, 12–15 × 2–3.5 µm, with gelatinous appendages at both ends, 13–25 µm long but in squash mounts quickly growing to 70 µm or more. Microconidia fusiform, non-septate, 3–4 × 1–1.5 µm.

Chemistry: No substances detected by TLC.

Ecology and distribution: This species is known from several collections from the type locality and its vicinity in South China. It grows on leaves in wet tropic forest.

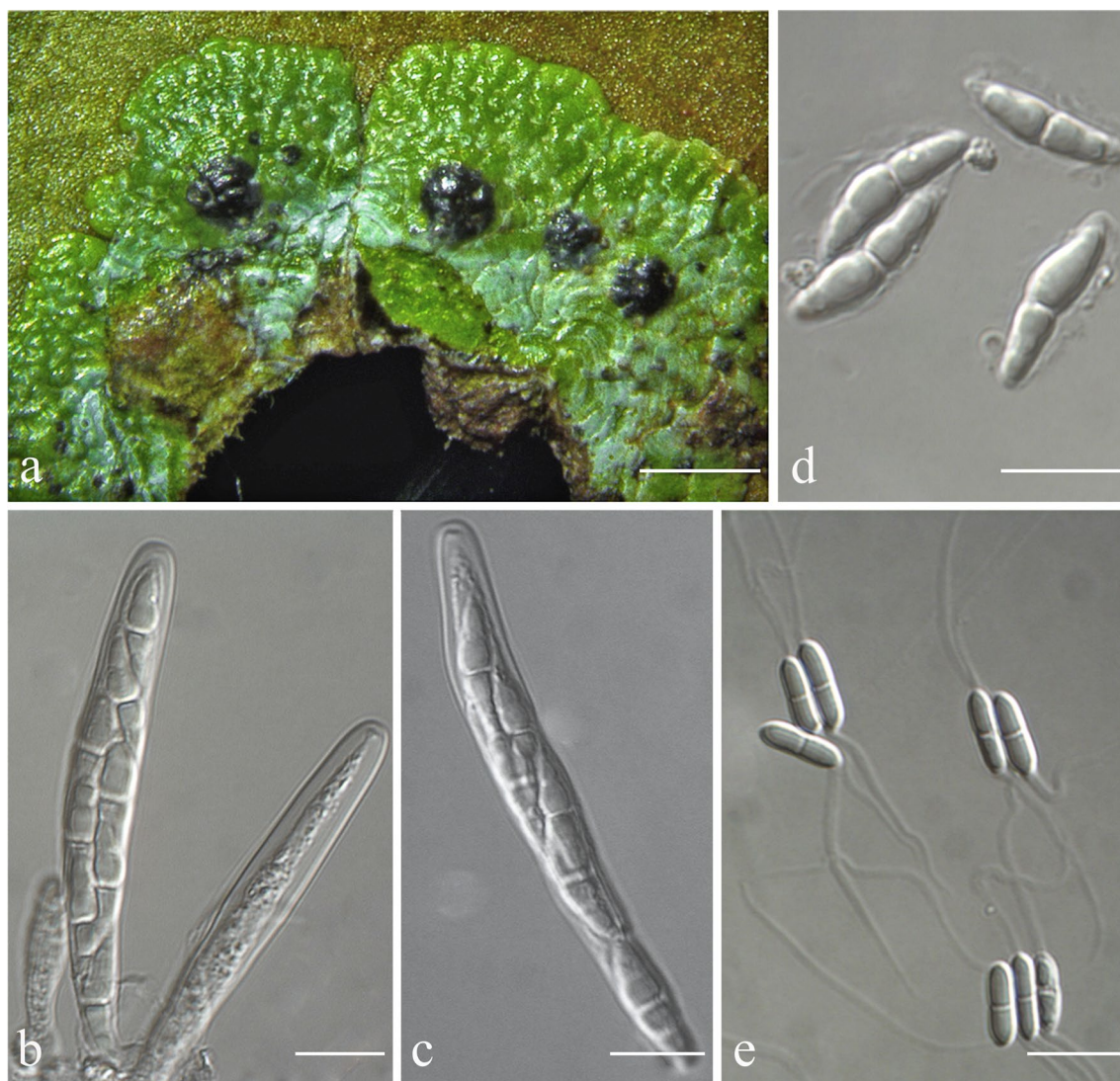


Fig. 9 *Seriauxiella flagellata* sp. nov. (holotype, HMAS-L0139216) **a** Thallus **b–c** Asci **d** Ascospores **e** Macroconidia with long appendages. Scale bars: **a** = 600 µm, **b–e** = 10 µm

Notes: This new species is very similar to *Seriauxiella filifera* and the only tangible difference appears to be the shorter asci. The differences in the ITS are, however, substantial, with an overall similarity of only 95.6% (see above).

Additional specimens examined. CHINA. Hainan, Ledong County, Jianfengling, Mingfenggu; 18° 44' 32" N, 108° 50' 32" E, 985 m; on living leaves; 12 December 2014, J.H. Wang & R.D. Liu HN2014287 (HMAS-L0130616); *ibid.*, 18° 44' 5" N, 108° 52' 8" E, 920 m; on living leaves; 11 December 2014, J.H. Wang & R.D. Liu HN2014191_3 (HMAS-L0141611), HN2014191_4 (HMAS-L0141612); *ibid.*, 18° 44' 36" N, 108° 50' 39" E, 962 m; on living leaves; 12 December 2014, J.H. Wang & R.D. Liu HN2014231_7 (HMAS-L0141605).

3. *Raciborskiella* Höhn., Sber. Akad. Wiss. Wien, Math.-Naturw. Kl., Abt. 1 118: 1176 (1909).

Mycobank: MB 4636

Type species: *Raciborskiella talaumae* (Racib.) Höhn.

Description: Thallus foliicolous, subcuticular, hypophyllous, dispersed into rounded, partly confluent patches with entire margins, very thin, usually dark bluish grey. Photobiont *Cephaleuros*. Perithecia fully exposed, prominent, more or less conical, not covered by thallus, black; excipulum prosoplectenchymatous, colorless; involucrellum carbonized, black; hamathecium colorless, I–, KI–; paraphyses slightly branched and anastomosing. Asci bitunicate, with short tholus and narrow ocular chamber, I–, KI–, clavate to oblong. Ascospores 8 per ascus, biserial to irregular arranged, fusiform, 1-septate, colorless, rather large,



Fig. 10 *Serusiauxiella sinensis* sp. nov. (holotype, HMAS-L0141614) **a** Thallus, **b** Asci, **c** Ascospores, **d** Macroconidia showing the long-grown appendages. Scale bars: **a**=600 μ m, **b–d**=10 μ m

30–70 $\times$ 5–7 μ m, strongly constricted at the septum and frequently breaking into part spores, both ends sometimes with thin, gelatinous appendages. Pycnidia adnate, wart-shaped to conical, black. Macroconidia bacillar to filiform, 1-septate, colorless, both ends with short to medium-sized, gelatinous appendages (not exceeding 50 μ m even after prolonged time in squash mounts). Microconidia fusiform-ellipsoid, non-septate, colorless.

Chemistry: No substances detected by TLC.

Notes: *Raciborskiella* was kept as a separate genus by Santesson (1952) and various subsequent workers (Singh 1970; Vézda 1984; Roux and Sérusiaux 1995; Sérusiaux

and Polly 1996), with two species growing hypophyllous. This classification was not accepted in more recent treatments, which subsumed *Raciborskiella* within *Strigula* s.lat. (Harris 1995; Lücking 2008; McCarthy 2009a). Our data show that the two species previously included in this genus by Santesson (1952) are not closely related, with *Strigula prasina* clustering within *Strigula* s.str. This is in accordance with substantial anatomical differences between the two taxa (Santesson 1952; Lücking 2008). On the other hand, *R. janeirensis* sensu Santesson (1952) corresponds to two phylogenetically distinct species, differing in ascospore size, *R. janeirensis* s.str. and *R. talaumae*, the type of the genus.

On account of the phylogenetic analysis and the unique morpho-anatomical characters (very thin, bluish grey thallus, branched and anastomosing paraphyses, large and strongly constricted ascospores sometimes with thin appendages; see also Roux and Sérusiaux 1995), the genus *Raciborskiella* is here resurrected, but its hypophyllous growth is not a diagnostic feature. Except for *Raciborskiella* s.str., ascospore appendages have so far only been reported from one species currently placed in *Strigula* s.str., *S. kaitokensis* Sérusiaux & Polly, but are definitely absent in most species of *Strigula* s.str. and the other foliicolous genera distinguished here (see also Sérusiaux and Polly 1996).

Key to species of *Raciborskiella*

1. Ascospores 30–40 µm long; paleotropical *Raciborskiella talaumae*
1. Ascospores 40–70 µm long; chiefly neotropical *Raciborskiella janeirensis*

Raciborskiella talaumae (Racib.) Höhn., Sber. Akad. Wiss. Wien, Math.-Naturw. Kl., Abt. 1 118: 1176 (1909). Fig. 11

Basionym: *Clypeolum talaumae* Racib., Parasit. Alg. Pilze Java's (Jakarta) 3: 35 (1900).

Type: INDONESIA. Java: Goenoeng Pantjar; Raciborski s.n. (holotype, KRA, not seen).

Description. Thallus subcuticular, hypophyllous, dispersed into rounded to partly confluent patches, often occurring along the leaf nerves and margins, 2–15 mm across and 7–15 µm thick, dark grey-green to bluish grey. Photobiont a species of *Cephaleuros*, cells 7–12 × 5–10 µm. Perithecia completely exposed, prominent, wart-shaped to conical, 0.3–0.6 mm diam and 60–150 µm high, black; excipulum prosoplectenchymatous, 12–18 µm thick, colorless to brown; involucrellum carbonized, 12–20 µm thick, black; paraphyses slightly branched and anastomosing. Asci oblong, 90–105 × 12–15 µm. Ascospores biserial to irregularly arranged, oblong to fusiform, 1-septate, 30–40 × 5–7 µm, with strong constriction at the septum and usually breaking into parts within the asci, both ends sometimes with thin, terminal gelatinous appendages. Pycnidia wart-shaped, those producing macroconidia 0.15–0.2 mm, those producing microconidia 0.05–0.1 mm, black. Macroconidia bacillar, 1-septate, 10–13 × 2.5–5 µm. Microconidia fusiform, non-septate, 3–5 × 1 µm.

Chemistry: No substances detected by TLC.

Distribution and ecology: This species is apparently eastern paleotropical, known from the type from Indonesia (Java) and from mainland China, there found in humid, semiexposed forest habitats.

Notes: *Raciborskiella talaumae* differs from *R. janeirensis* in ascospore size, those of the latter being 40–70 µm

long. Santesson (1952) considered the ascospore measurements of *R. talaumae* to refer to young ascospores, but our material and the molecular data clearly set the two species apart. *Melanopsamma areolatum* Rehm from Brazil was also described as having shorter ascospores (30–36 µm), but Santesson annotated the type as having 35–52 µm long ascospores, thus in the range of *R. janeirensis* and a synonym of the latter.

Specimens examined. CHINA. Hainan: Baoting County, Qixianling National Nature Reserve; 18° 42' 21" N, 109° 42' 14" E, 350 m; on living leaves; 7 September 2017, S.H. Jiang HN20171643 (HMAS-L0139627), HN20171510 (HMAS-L0139628), HN20171246 (HMAS-L0139624), HN20171534 (HMAS-L0139629), HN20171523 (HMAS-L0139626), HN20171258 (HMAS-L0139625).

4. *Puiggariella* Speg., Anal. Soc. Cient. Argent. 12(3): 99 (1881).

MycoBank: MB 4546

Type species: *Puiggariella apiahyna* Speg. [= *Puiggariella nemathora* (Mont.) S.H. Jiang, Lücking & J.C. Wei].

Description: Thallus foliicolous, subcuticular, with entire margins or crenulate-lobulate to lacinate, lobes widely separated to completely confluent, surface usually with numerous minute, white papillae. Photobiont *Cephaleuros*. Perithecia immersed-erumpent to prominent, wart-shaped to applanately conical, often ridged or fissured; excipulum prosoplectenchymatous, colorless; involucrellum colorless to pale brown, not carbonized; hamathecium colorless, I–, KI–; paraphyses unbranched, thin. Asci bitunicate, with short tholus and narrow, ocular chamber, I–, KI–, clavate to oblong. Ascospores 8 per ascus, uniseriate to biserial, fusiform, 1-septate, colorless, 15–25 × 4–6 µm. Pycnidia immersed-erumpent, wart-shaped to conical, pale to brownish. Macroconidia bacillar to filiform, 1-septate, colorless, both ends usually with short to medium length gelatinous appendages (usually not exceeding 40 µm even after prolonged time in squash mounts). Microconidia fusiform-ellipsoid, non-septate, colorless.

Chemistry: No substances detected by TLC.

Notes: The species included in this small genus are quite characteristic due to their thallus morphology (often lacinate and with white papillae) and the uncarbonized perithecia which often feature ridges or fissures. Spegazzini (1881) did not recognize the distinctiveness of this lineage, nor did he realize that he dealt with a lichenized fungus, and Santesson (1952) included what he believed to be a single species within *Strigula*. Based on our data, we currently distinguish three species.

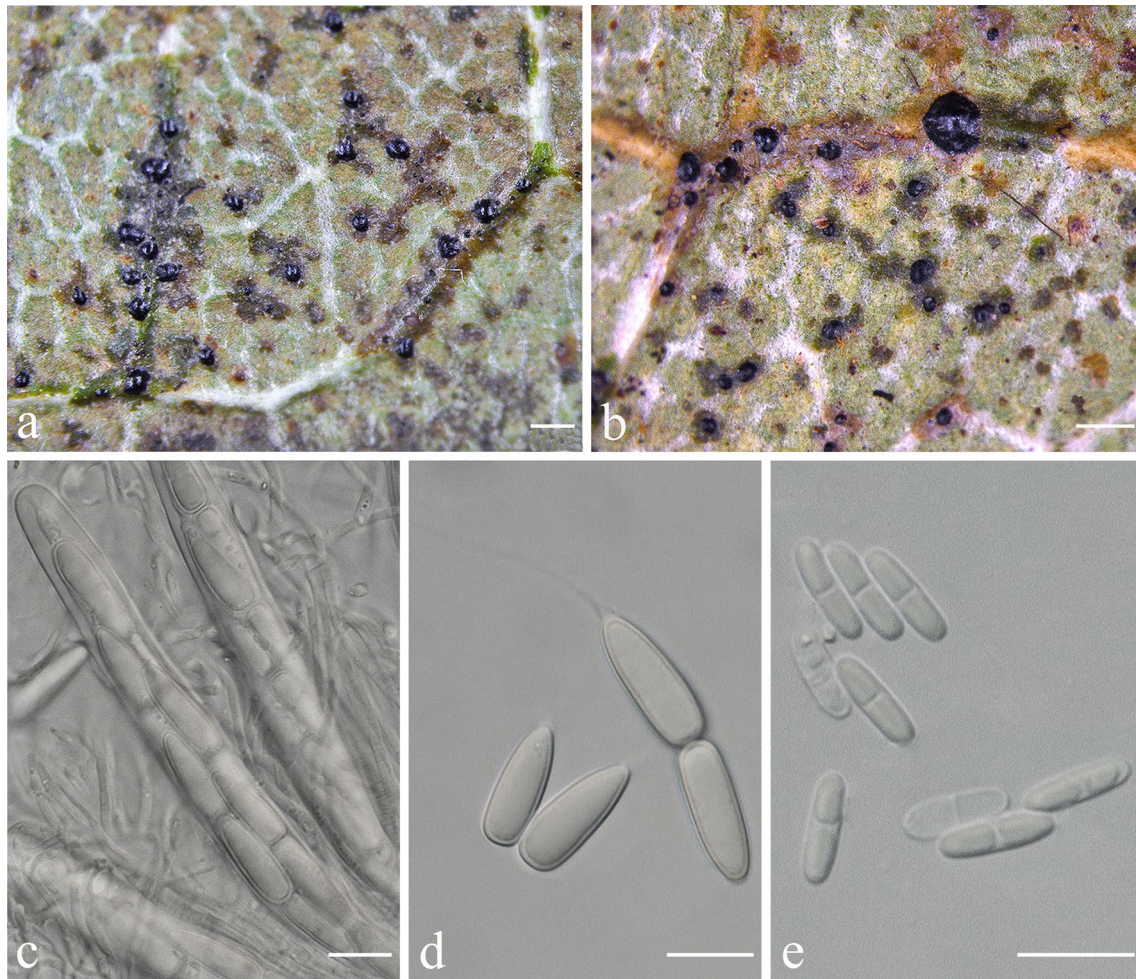


Fig. 11 *Raciborskiella talaumae* **a** Thallus (HMAS-L0139627), **b** Thallus (HMAS-L0139628), **c** Asci (HMAS-L0139627), **d** Ascospores (HMAS-L0139627), **e** Macroconidia (HMAS-L0139628). Scale bars: **a**, **b** = 500 µm, **c**, **e** = 10 µm

Key to species of *Puiggariella*

1. Thallus lobes indistinct and irregular, only visible marginally, otherwise the thallus appearing mostly entire; surface with scattered, minute papillae *Puiggariella confluens*
1. Thallus lobes distinct, becoming lacinate and in part leaving interspaces, irregular to regularly radiating; lobe margins with numerous, minute papillae 2
2. Thallus lobes regularly radiating, slightly separate to contiguous *Puiggariella nigrocincta*
2. Thallus lobes irregular, often widely spaced *Puiggariella nemathora*

Puiggariella confluens (Müll. Arg.) S.H. Jiang, Lücking & J.C. Wei, **comb. et stat. nov.** Fig. 12

Mycobank: MB 833575

Basionym: *Strigula argyronema* var. *confluens* Müll. Arg., Bull. Soc. R. Bot. Belg. 30(1): 88 (1891).

Type: COSTA RICA. Alajuela: Môle de San Rafael; 1899; H. Pittier 5162 (holotype, G-G00292244!)

Description. Thallus subcuticular, lobulate-crenulate, with short, rounded, confluent lobes, 4–15 mm across and 30–50 µm thick, surface usually with numerous minute, white papillae. Photobiont a species of *Cephaleuros*, cells 8–13 × 4–7 µm. Perithecia erumpent to prominent, covered by a thick thallus layer up to ostiole, wart-shaped, 0.5–0.9 mm diam. and 100–250 µm high, pale greenish grey to white, ridged; excipulum prosoplectenchymatous, 12–25 µm thick, colorless; involucrellum confluent with excipulum, 35–75 µm thick, colorless to pale brown; paraphyses unbranched. Asci oblong, 75–110 × 7.5–10 µm. Ascospores uniseriate, fusiform, 1-septate, with constriction at septum, 17–20 × 4–5 µm. Pycnidia producing macroconidia immersed-erumpent, wart-shaped, 0.1–0.15 mm, black. Macroconidia bacillar, 1-septate, 10–13 × 2.5–3.7 µm, with appendages at both

ends 15–30 μm long. Pycnidia producing microconidia not seen.

Chemistry: No substances detected by TLC.

Notes. This taxon is here elevated to species level, as it differs from typical *Puiggariella nemathora* in the marginally confluent lobes.

Additional specimens examined. COSTA RICA. Cartago: Orosi valley; 09°47' N, 83°51' W, 1150 m; coffee plantations and secondary vegetation, on leaves; 1991, R. Lücking 6a-2 (B-600205073), 6a-3 (B600205074). GUATEMALA. Izabal: Quiriguá; 15°16'10"N, 89°02'25"W, 75 m; secondary vegetation around Maya archaeological site, on leaves; December 1991, R. Lücking 4524 (B-600205040).

Puiggariella nemathora (Mont.) S.H. Jiang, Lücking & J.C. Wei, **comb. nov.** Fig. 13

MycoBank: MB 833579

Basionym: *Strigula nemathora* Mont. in Sagra, Historia Física, Política y Natural de la Isla de Cuba 9: 96 (1845).

Type: CUBA. Unknown locality; Auber s.n. or de la Sagra s.n. (holotype, PC!).

Description. Thallus subcuticular, lobulate, with elongate to lacinate, usually diverging lobes leaving interspaces, 5–30 mm across and 30–50 μm thick, lobe margins with numerous minute, white papillae. Photobiont a species of *Cephaleuros*, cells 8–14 $\times$ 4–7 μm . Perithecia erumpent to prominent, covered by a thick thallus layer up to ostiole, wart-shaped, 0.5–1 mm diam. and 150–250 μm high, pale greenish grey to white, ridged; excipulum

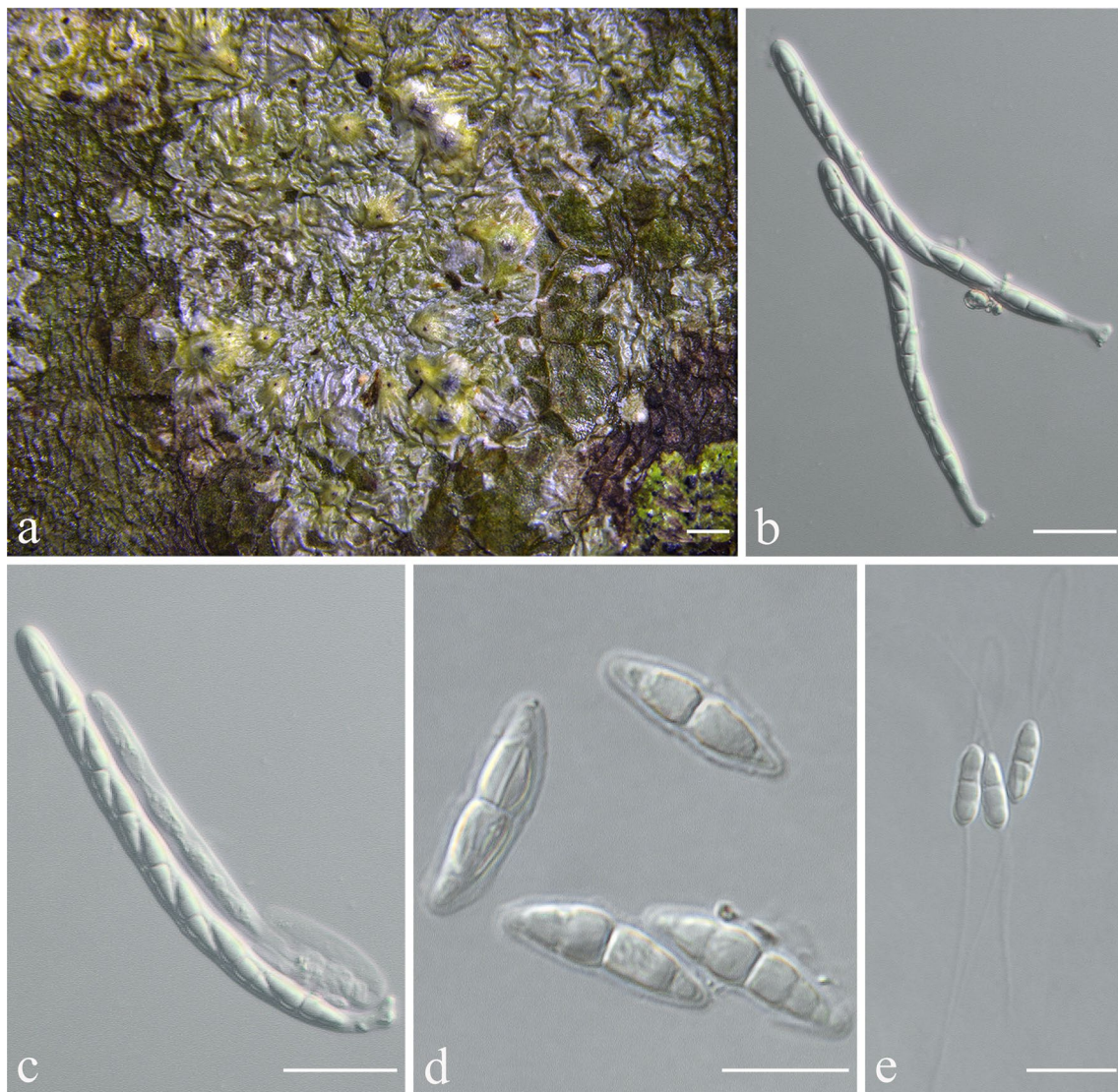


Fig. 12 *Puiggariella confluens* comb. nov. (B-600205074) **a** Thallus, **b–c** Asci, **d** Ascospores, **e** Macroconidia. Scale bars: **a**=500 μm , **b**, **c**=20 μm , **d–e**=10 μm

prosoplectenchymatous, 12–25 μm thick, colorless; involucrellum confluent with excipulum, 30–70 μm thick, colorless to pale brown; paraphyses unbranched. Asci oblong, 80–110 $\times$ 7–10 μm . Ascospores uniseriate to irregularly arranged, fusiform, 1-septate, with constriction at septum, 17–22 $\times$ 4–6 μm . Pycnidia producing macroconidia immersed-erumpent, wart-shaped, 0.1–0.15 mm, black. Macroconidia bacillar, 1-septate, 9–13 $\times$ 2.5–3.5 μm , with appendages at both ends 15–30 μm long. Microconidia fusiform, non-septate, 3–5 $\times$ 1.3–1.7 μm .

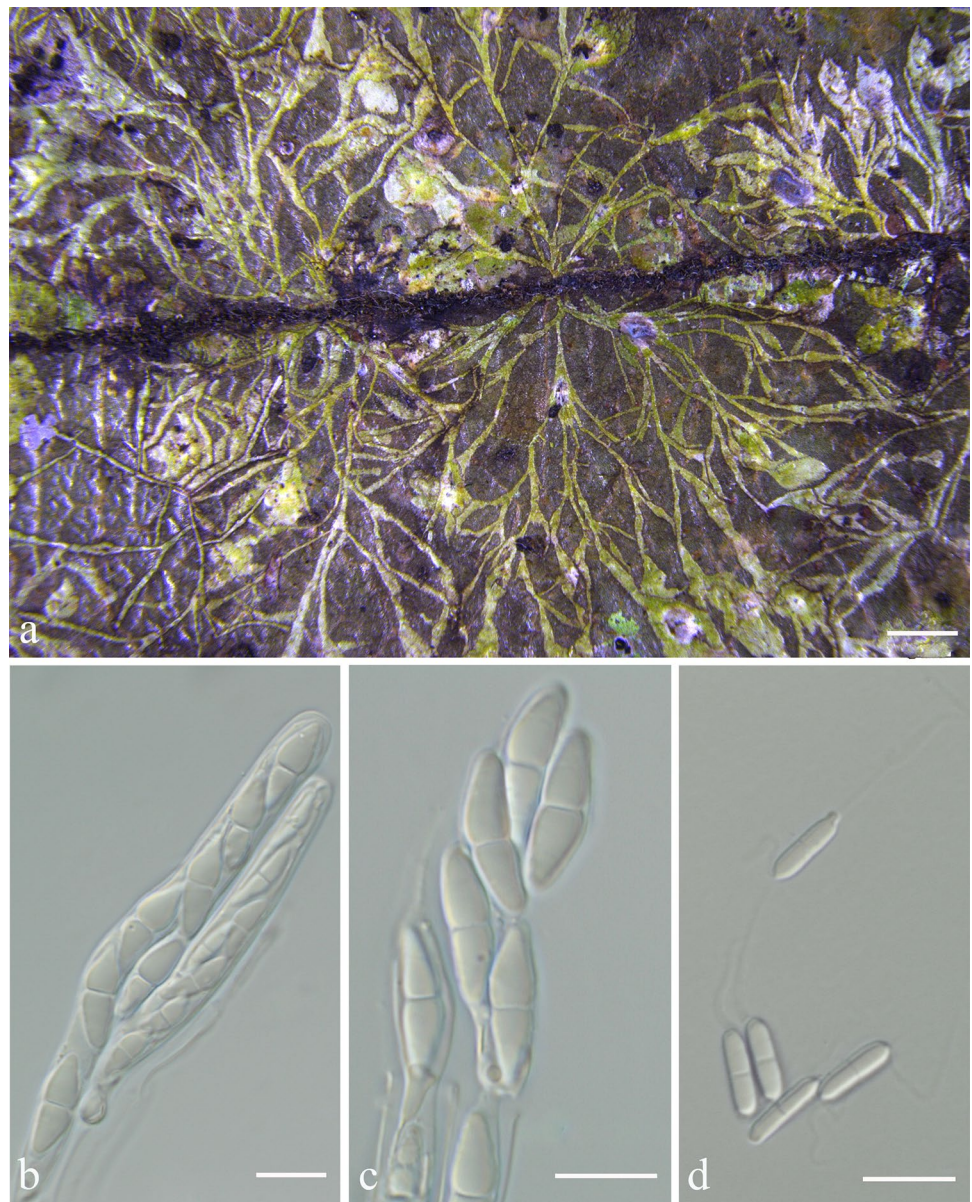
Chemistry: No substances detected by TLC.

Distribution and ecology: The distribution of *Strigula nemathora* is difficult to ascertain, but it may deal with a neotropical taxon, as this morphotype is mostly known from that region.

Notes: The name *Strigula nemathora* is here restricted to a taxon with distinctly laciniate, often widely spaced lobes, a frequent morphotype commonly found in the Neotropics (Lücking 2008). More data are required to disentangle this species complex and evaluate the status of the various synonyms of *S. nemathora* proposed by Santesson (1952).

Additional specimens examined. BRAZIL. Paraiba: Mamanguape, Reserva Biológica Guaribas; 06° 44' 59" S, 41° 07' 11" W, 204 m; Atlantic forest, on leaves; October 2014, A.B. Xavier-Leite 1586 (ISE-32586). Sergipe: Itabaiana, Parque Nacional Serra de Itabaiana; 10° 42' 36" S, 37° 16' 42" W, 400–660 m; Atlantic forest, on leaves; A.B. Xavier-Leite 1794 (ISE-32794).

Fig. 13 *Puiggariella nemathora* comb. nov. (ISE-32794) **a** Thallus, **b**, **c** Asci and ascospores, **d** Macroconidia. Scale bars: **a** = 2 mm, **b–d** = 10 μm



Puiggariella nigrocincta (Müll. Arg.) S.H. Jiang, Lücking & J.C. Wei, **comb. nov.** Fig. 14

MycoBank: MB 833581

Basionym: *Strigula nigrocincta* Müll. Arg., Hedwigia 30: 187 (1891).

Type: VIETNAM. “Tonkin”, Mont Ba Vi; 1889, B. Balansa 3 (holotype, G-G00292245!).

Description. Thallus subcuticular, lobulate, with elongate to lacinate, separate to confluent, regularly radiating lobes, 5–15 mm across and 30–50 µm thick, lobe margins with numerous minute, white papillae. Photobiont a species of *Cephaleuros*, cells 8–15 × 5–8 µm. Perithecia erumpent to prominent, covered by a thick thallus layer up to ostiole, wart-shaped, 0.3–0.6 mm diam. and 150–200 µm high, pale greenish grey to white, ridged; excipulum prosoplectenchymatous, 15–25 µm thick, colorless; involucrellum confluent with excipulum, 30–50 µm thick, colorless to pale brown; paraphyses unbranched. Asci oblong, 80–100 × 7–10 µm. Ascospores irregularly biserial, fusiform, 1-septate, with constriction at septum, 17–22 × 4–6 µm. Pycnidia producing macroconidia immersed-erumpent, wart-shaped, 0.1–0.15 mm, black. Macroconidia bacillar, 1-septate,

9–13 × 2.5–3.5 µm, with appendages at both ends 15–30 µm long. Microconidia fusiform, non-septate, 3–5 × 1.3–1.7 µm.

Chemistry: No substances detected by TLC.

Distribution and ecology: This is likely an eastern pantropical species, thus far known from Vietnam and (sub-) tropical southern China.

Notes: Based on our molecular data, *Strigula nemathora* s.lat. as defined by Santesson (1952) comprises more than one species. The two sequenced clades differ in thallus morphology and distribution. We have therefore restricted the name *S. nemathora* to the neotropical material with typically separate, somewhat irregular laciniae and take up the name *S. nigrocincta* for the eastern paleotropical material with radiating, more contiguous lobes. The material from China is quite uniform in this respect and agrees well with the type from China. The epithet *nigrocincta* is a bit misleading, as it refers to the blackened area of the leaf around the thalli. This effect is likely phorophyte-specific and not a feature of the lichen.

Additional specimens examined. CHINA. Guangxi: Longzhou County, Nonggang National Nature Reserve; 22° 27' 55" N, 106° 57' 5" E, 270 m; on living leaves; 3 December

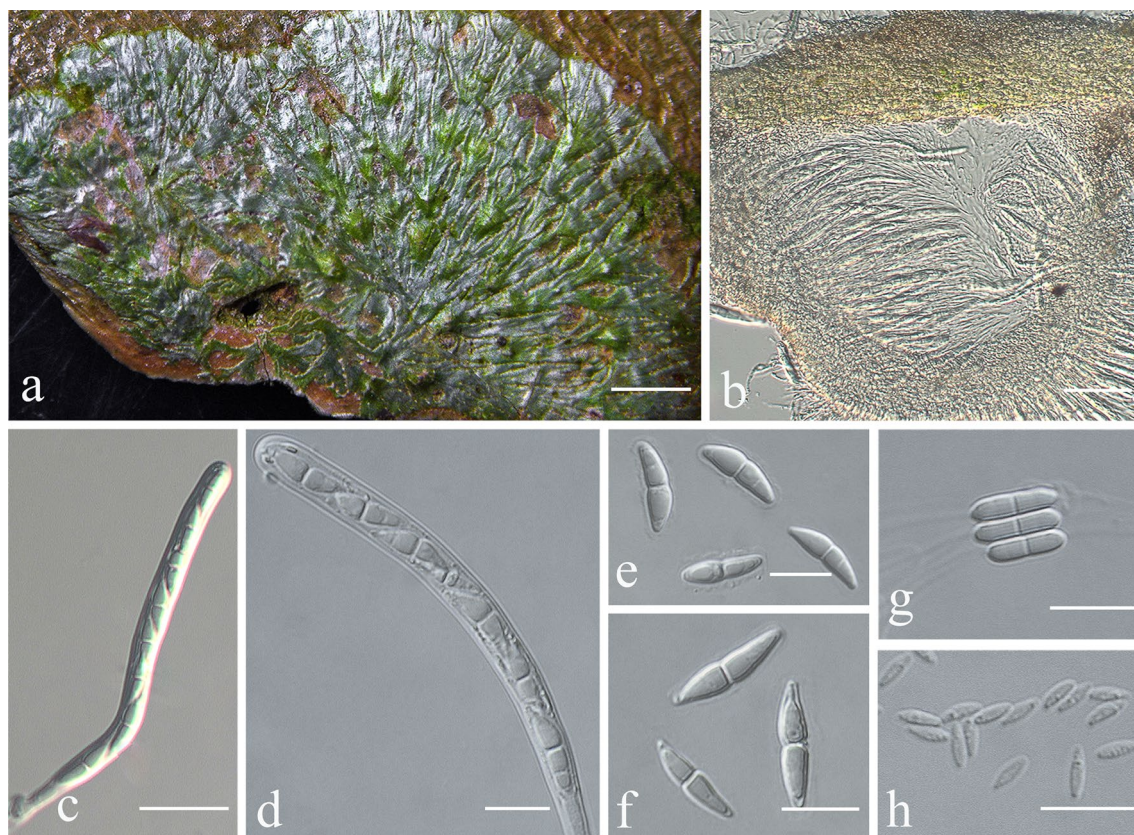


Fig. 14 *Puiggariella nigrocincta* comb. nov. **a** Thallus (HMAS-L0141549), **b** Perithecia (HMAS-L0141533), **c**, **d** Asci (HMAS-L0141533), **e**, **f** Ascospores (HMAS-L0141533), **g** Macroconidia

(HMAS-L0141544), **h** Microconidia (HMAS-L0141544). Scale bars: **a** = 500 µm, **b** = 50 µm, **c** = 20 µm, **d–h** = 10 µm

2015, S.H. Jiang, GX201511241 (HMAS-L0139287), GX201511249 (HMAS-L0139231), GX201511252 (HMAS-L0139232). Yunnan: Xishuangbanna, Mengla County, tropical botanical garden of Chinese Academy of Sciences, East area; 21° 55' 39" N, 101° 15' 52" E, 560 m; on living leaves; 18 November 2015, X.L. Wei & S.H. Jiang XTBG2015005 (HMAS-L0139341), XTBG2015008 (HMAS-L0139385), XTBG2015011_1 (HMAS-L0139332), XTBG2015011_2 (HMAS-L0141530), XTBG2015024_1 (HMAS-L0139348), XTBG2015024_3 (HMAS-L0141532), XTBG2015024_4 (HMAS-L0141533), XTBG2015025_2 (HMAS-L0139334), XTBG2015028 (HMAS-L0139335), XTBG2015029_2 (HMAS-L0141534), XTBG2015030_1 (HMAS-L0139350), XTBG2015030_2 (HMAS-L0141535), XTBG2015030_3 (HMAS-L0141536), XTBG2015038_1 (HMAS-L0141537), XTBG2015042 (HMAS-L0139336), XTBG2015044 (HMAS-L0139356), XTBG2015050_1 (HMAS-L0139360), XTBG2015050_2 (HMAS-L0141539), XTBG2015059_1 (HMAS-L0139363), XTBG2015059_4 (HMAS-L0141540), XTBG2015059_5 (HMAS-L0141541), XTBG2015059_6 (HMAS-L0141542), XTBG2015059_7 (HMAS-L0141543), XTBG2015059_8 (HMAS-L0141544), XTBG2015059_9 (HMAS-L0141545), XTBG2015059_10 (HMAS-L0141546), XTBG2015061_2 (HMAS-L0139396), XTBG2015061_3 (HMAS-L0141547), XTBG2015061_4 (HMAS-L0141548), XTBG2015064 (HMAS-L0139366), XTBG2015064_3 (HMAS-L0141549), XTBG2015064_4 (HMAS-L0141550), XTBG2015065_5 (HMAS-L0141552), XTBG2015065_6 (HMAS-L0141553), XTBG2015065_7 (HMAS-L0141554), XTBG2015065_8 (HMAS-L0141555), XTBG2015065_9 (HMAS-L0141556), XTBG2015066_1 (HMAS-L0139368), XTBG2015066_3 (HMAS-L0141557), XTBG2015066_4 (HMAS-L0141558), XTBG2015066_5 (HMAS-L0141559), XTBG2015066_6 (HMAS-L0141562), XTBG2015066_7 (HMAS-L0141563), XTBG2015067_1 (HMAS-L0139369), XTBG2015067_4 (HMAS-L0141561), XTBG2015067_5 (HMAS-L0141567), XTBG2015067_6 (HMAS-L0141564), XTBG2015069_1 (HMAS-L0139370), XTBG2015069_2 (HMAS-L0141565), XTBG2015069_4 (HMAS-L0141566), XTBG2015070_3 (HMAS-L0139371), XTBG2015071 (HMAS-L0139372), XTBG2015074_2 (HMAS-L0139373), XTBG2015074_3 (HMAS-L0141568), XTBG2015074_4 (HMAS-L0141568), XTBG2015075_2 (HMAS-L0139374), XTBG2015076 (HMAS-L0139375), XTBG2015077_4 (HMAS-L0139376); *ibid.*; 21° 54' 35" N, 101° 16' 52" E, 626 m; on living leaves; 18 November 2015, X.L. Wei & S.H. Jiang XTBG2015099_3 (HMAS-L0141570), XTBG2015118 (HMAS-L0139337). Jinghong County; 794 m; on living leaves; 19 November 2015, X.L. Wei & S.H. Jiang XTBG2015123_2 (HMAS-L0139340); *ibid.*; 22° 19' 15" N, 100° 47' 13" E, 968 m; on living leaves; 28 October 2016, X.Y. Liu YN20160082 (HMAS-L0139194), YN20160087 (HMAS-L0139188),

YN20160093 (HMAS-L0139189); *ibid.*; 21° 59' 04" N, 101° 09' 31" E, 941 m; on living leaves; 26 October 2016, YN20160146 (HMAS-L0139187).

5. *Racoplaca* Fée, Essai Crypt. Exot. (Paris): lxxviii, xciv, xcix (1825) [1824].

Mycobank: MB 4640

Type species. Racoplaca subtilissima Fée.

Description: Thallus foliicolous, crustose, subcuticular, typically laciniate, composed of dichotomously branched lobes that form an attractively patterned radiating reticulum, individual lobes bordered by thin, black line. Photobiont *Cephaleuros*. Perithecia prominent, wart-shaped to conical, usually covered by a thin thallus layer up to the ostiole, therefore not pure black; excipulum prosoplectenchymatous, colorless; involucrellum carbonized, black; hamathecium colorless, I–, KI–; paraphyses unbranched, thin. Asci bitunicate, with short tholus and narrow, ocular chamber, I–, KI–, clavate to oblong. Ascospores 8 per ascus, biserial or irregularly arranged, oblong to fusiform, 1-septate, colorless, 10–25 × 2–5 µm. Pycnidia immersed-erumpent to adnate, wart-shaped to conical, usually black. Macroconidia bacillar to filiform, 1-septate, colorless, both ends with short gelatinous appendages (10–25 µm, not exceeding 50 µm even after prolonged time in squash mounts). Microconidia fusiform-ellipsoid non-septate, colorless.

Chemistry: No substances detected by TLC.

Notes: The genus *Racoplaca* is here reinstated for the species of the *Strigula subtilissima* group, characterized by thin, laciniate thalli with the margins bordered by a thin, black line. The genus is both phylogenetically and phenotypically distinctive. Besides the type species, the genus includes four further taxa.

Key to species of *Racoplaca*

1. Ascospores fusiform, 14–23 × 3–5 µm2
1. Ascospores oblong, 8–18 × 2–3 µm3
2. Perithecia hemispherical to conical, up to 0.7 mm diam., greyish black*Racoplaca melanobapha*
2. Perithecia wart-shaped to hemispherical, up to 0.4 mm diam., upper part exposed and black*Racoplaca tremens*
3. Thallus dark green, with indistinct, mostly confluent laciniae..... *Racoplaca maculata*
3. Thallus greenish brown to olive, with distinct, radiating laciniae..... 4
4. Laciniae thickened, with conspicuous transverse undulations*Racoplaca transversoundulata*
4. Lacinia thin, with even surface.....*Racoplaca subtilissima*

Racoplaca maculata (Cooke & Massee) S.H. Jiang, Lücking & J.C. Wei, **comb. nov.**

Mycobank: MB 833584

Basionym: *Micropeltis maculata* Cooke & Massee, in Cooke, *Grevillea* 18(86): 35 (1889).

Type: BRAZIL. Rio de Janeiro: Near Rio de Janeiro; 1889, Glaziou 18093 (lectotype, BM ex K!; Santesson 1952, p. 186).

Racoplaca melanobapha (Kremp.) S.H. Jiang, Lücking & J.C. Wei, **comb. nov.** Fig. 15

Mycobank: MB 833586

Basionym: *Strigula melanobapha* (Kremp.) R. Sant., *Symb. bot. ups. l.* 12 (no. 1): 188 (1952).

Type: MALAYSIA. Sarawak: Borneo; 1866, Beccari 219 (holotype, M-0067744!).

Description: Thallus subcuticular, typically lacinate, forming thin, radiating, sometimes confluent lobes, individual lobes bordered by thin, black, interrupted line, 10–50 mm across and 10–15 µm thick. Photobiont *Cephaleuros*, cells angular-rounded, 9–13 × 4–7 µm.

Perithecia exposed, covered by thin thallus, wart-shaped to conical, 0.4–0.7 mm diam. and 130–250 µm high, greyish black; Excipulum prosoplectenchymatous, 10–20 µm thick, color less to brown; Involucrellum carbonaceous, 30–50 µm thick, black. Asci narrowly obclavate, 70–110 × 6–10 µm. Ascospores irregularly biserial, fusiform, 1-septate, with constriction at septum, 14–22 × 3–5 µm. Pycnidia wart-shaped, those producing macroconidia 0.2–0.3 mm, those producing microconidia 0.1–0.2 mm diam., black. Macroconidia bacillar, non-septate, 10–12 × 2–3 µm, with appendages at both ends 15–25 µm long. Microconidia fusiform, non-septate, 4–6 × 1.5–2 µm.

Chemistry: No substances detected by TLC.

Distribution and ecology: This is presumed to be a pantropical species; it has been reported from Guiana, Peru, French Guiana, Brazil, Sierra Leone, and Borneo (Santesson 1952; Lücking 2008).

Notes: *Racoplaca melanobapha* is characterized by thallus composed of dichotomously branched lobes bordered by a thin, black, interrupted line that form an attractively patterned reticulum. *Racoplaca subtilissima* differs in the

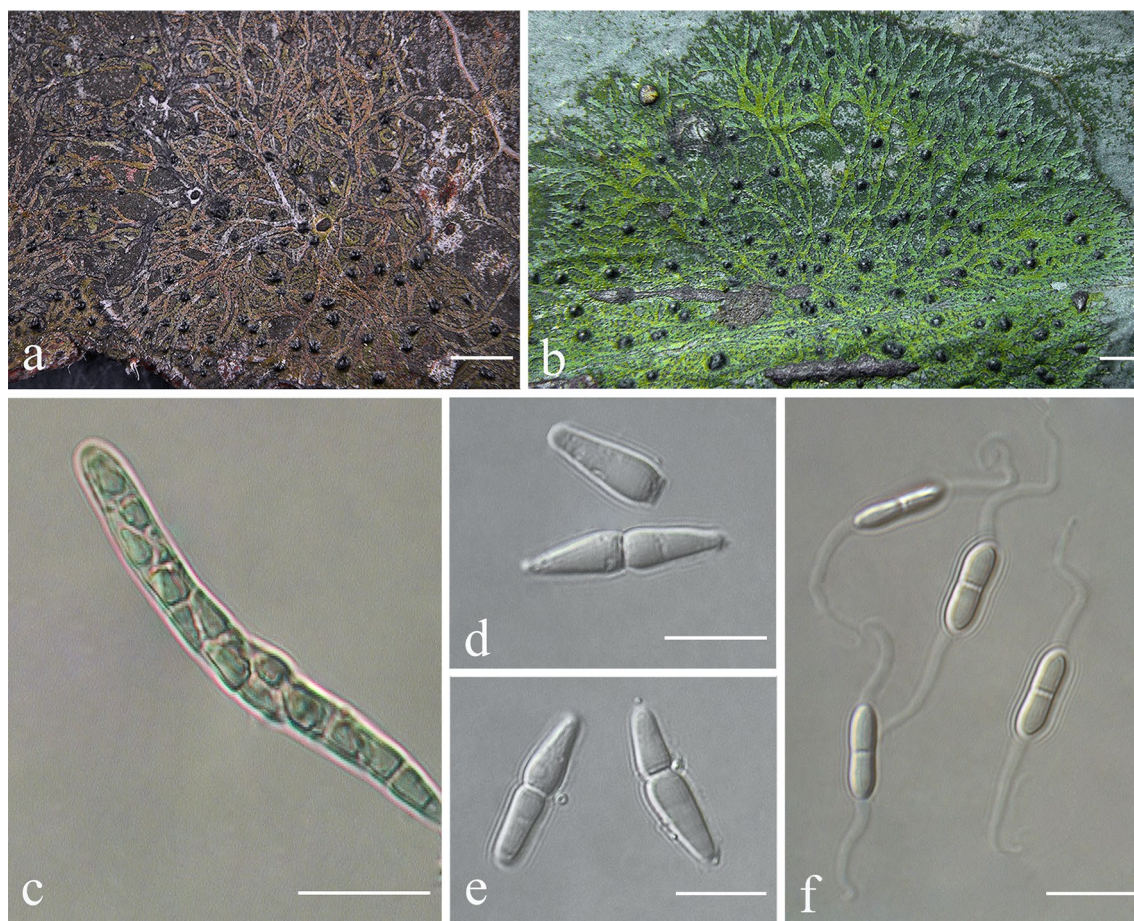


Fig. 15 *Racoplaca melanobapha* comb. nov. **a** Thallus (HMAS-L0139275), **b** Thallus (HMAS-L0139276), **c** Asci (HMAS-L0139275), **d–e** Ascospores (HMAS-L0139331), **f** Macroconidia (HMAS-L0139275). Scale bars: **a** = 500 µm, **b** = 600 µm, **c** = 20 µm, **d–f** = 10 µm

smaller, narrower, oblong ascospores and the continuous black line, whereas *R. maculata* has a dark green thallus with short lobes. *Racoplaca tremens* has much smaller perithecia basally covered by a thick, thallus layer, apically exposed and pure black.

Additional specimens examined. CHINA. Guangdong: Ruyuan County, Nanling National Forest Park; 24° 54' 59" N, 113° 2' 5" E, 848 m; on living leaves; 17 May 2015, X.L. Wei & J.H. Wang GD2015066_3 (HMAS-L0141593); *ibid.*; 24° 56' 59" N, 112° 56' 02" E, 1257 m; on living leaves; 17 May 2015, X.L. Wei & J.H. Wang GD2015070 (HMAS-L0139173). Guangxi, Shangsi County, Shiwan Mountain Forest Park, along the way to Yingkesong and Jiulongsong; 21°53'46" N, 107° 53' 59" E, 636 m; on living leaves; 25 May 2015, X.L. Wei & J.H. Wang GX20150355 (HMAS-L0139275), GX20150362 (HMAS-L0139276); *ibid.*; 24° 43' 27" N, 114° 15' 22" E, 345 m; on living leaves; 26 May 2015, X.L. Wei & J.H. Wang GX20150347 (HMAS-L0139331); *ibid.*; 21° 53' 8" N, 107° 54' 41" E, 657 m; on living leaves; 25 May 2015, X.L. Wei & J.H. Wang GX20150323 (HMAS-L0139328). Hunan: Chenzhou City, Mang Mountain National Nature Reserve; 24° 56' 59" N, 112° 56' 02" E, 1300 m; on living leaves; 13 September 2017, S.H. Jiang HN20170489 (HMAS-L0139623), HN20170535 (HMAS-L0139620). AUSTRALIA. Queensland: Mount Spec State Forest, Paluma Range 6 km W of Paluma; J.A. Elix 20250 & H. Streimann (CANB). Cook District, Kuranda; H. Streimann 61658 (CANB). Mossman Gorge, Daintree National Park, 6 km W of Mossman; H. Streimann 61677 p.p. (CANB).

Racoplaca transversoundulata (Sipman) S.H. Jiang, Lücking & J.C. Wei, **comb. nov.**

Mycobank: MB 833589

Basionym: *Strigula transversoundulata* Sipman in van den Boom & Sipman, *Folia Cryptog. Estonica* 53: 108 (2016).

Type: GUYANA. East Demerara District: Mabura Hill, near scientific field station c. 13 km S of the village; 5° 18' N, 58° 42' W, 100 m; undisturbed, c. 25 m tall forest on laterite on slope and in stream valley, foliicolous in undergrowth; 14 November 1992, H. Sipman 61761 (holotype, B 60 0200346!).

Racoplaca tremens (Müll. Arg.) S.H. Jiang, Lücking & J.C. Wei, **comb. nov.**

Mycobank: MB 833588

Basionym: *Strigula tremens* Müll. Arg., *Flora, Regensburg* 73: 200 (1890).

Type: BRAZIL. São Paulo: Apiaty; 1881, J.I. Puiggari s.n. (lectotype, G-G00126920!; Lücking 2008, p. 244).

6. *Phylloporis* Clem., *Gen. Fung.*: 41 (1909).

Mycobank: MB 4070

Type species: *Phylloporis phyllogena* (Müll. Arg.) Clem.

Description: Thallus typically foliicolous, rarely on smooth bark of twigs or petioles, supracuticular, easily separated from leaf, continuous to marginally dispersed or dissected, smooth, very thin, greenish to grey. Photobiont *Phycopeltis*, forming somewhat radiating networks of rectangular cells. Perithecia erumpent to adnate and prominent, lens-shaped to wart-shaped or conical; excipulum proso-plectenchymatous, colorless; involucrellum carbonized, black; hamathecium I–, KI–; paraphyses unbranched, thin. Asci bitunicate, with short tholus and narrow ocular chamber, I–, KI–, clavate to oblong. Ascospores 8 per ascus, biserial or irregularly arranged, fusiform, 1-septate, colorless, 7–15 × 2–3 µm. Pycnidia erumpent to adnate, wart-shaped to conical, usually black. Macroconidia bacillar to filiform, 1-septate, colorless, with short terminal appendages. Microconidia fusiform-ellipsoid non-septate, colorless.

Chemistry: No substances detected by TLC.

Notes: Species assigned to this genus were treated under the phylogenetically unrelated genus *Porina* by Santesson (1952), although he recognized the anatomical similarities with *Strigula* s.lat. Vězda (1984) resurrected the genus *Phylloporis* for this group and placed it close to *Strigula*, a classification accepted by subsequent workers (e.g. Lücking 1991). However, Harris (1995) subsumed the species within *Strigula* s.lat., a concept also followed by Lücking (2008). Our molecular data revealed *Phylloporis* as a distinct clade, which is accordance with its rather uniform phenotype features and the consistently supracuticular growth with a *Phycopeltis*-type photobiont. This underlines that while the photobiont itself cannot be considered a taxonomic feature of the mycobiont, the underlying selective mechanisms of the mycobiont to associate with that photobiont display a strong phylogenetic signal.

Besides the type, the genus includes seven further species, four of them already with names available in the genus: *Phylloporis multipunctata* (G. Merr. ex R. Sant.) Vězda, *P. obducta* (Müll. Arg.) R. Sant. & Tibell, *P. platypoda* (Müll. Arg.) Vězda, and *P. viridis* Lücking. For three additional species, new combinations are required which are introduced below. The only species thus far detected in China is *P. obducta*; however, this identification is provisional, given that the type is from Brazil and considering that other presumably pantropical taxa, such as *Strigula smaragdula*, apparently consist of several species (see above).

Key to species of *Phylloporis*

1. Thallus with numerous small, black dots; ascospores partly breaking into part spores..... 2
1. Thallus lacking black dots; ascospores remaining entire 3

2. Ascospores $12-16 \times 3.5-4.5 \mu\text{m}$
..... *Phylloporis multipunctata*
2. Ascospores $20-30 \times 4-6 \mu\text{m}$
..... *Phylloporis multipunctata*
3. Photobiont cells forming contiguous, regularly radiating plates..... 4
3. Photobiont cells forming irregular to somewhat radiating networks with interspaces 5
4. Perithecia radiately elongate and drop-shaped when seen from above, exposed and black *Phylloporis vulgaris*
4. Perithecia rounded with slightly spreading base, covered by distinct thallus layer, grey-green *Phylloporis viridis*
5. Perithecia covered by distinct thallus layer, grey-green, wart-shaped, up to $0.3(-0.4)$ mm diam. *Phylloporis obducta*
5. Perithecia exposed or covered by thin thallus layer, black to greyish black, contrasting with the thallus, conical or with expanded base (Mexican hat-shaped), $0.3-0.7$ mm diam. 6
4. Perithecia exposed or covered by thin thallus layer, black to greyish black, conical, $0.3-0.5$ mm diam. *Phylloporis phyllogena*
4. 4. Perithecia covered by thin thallus layer, greyish black, with expanded base (Mexican hat-shaped), $0.5-0.7$ mm diam..... *Phylloporis platypoda*

Phylloporis austropunctata (P.M. McCarthy) S.H. Jiang, Lücking & J.C. Wei, **comb. nov.**

Mycobank: MB 833571

Basionym: *Strigula austropunctata* P.M. McCarthy, Fl. Australia 57: 661 (2009).

Phylloporis cf. *obducta* (Müll. Arg.) R. Sant. & Tibell, Austrobaileya 2: 539 (1988).

Fig. 16

Mycobank: MB 134579

Basionym: *Phylloporina obducta* Müll. Arg., Flora 73: 198 (1890).

Type: BRAZIL. Rio de Janeiro: Near Rio de Janeiro; 1889, Glaziou 18086 (lectotype, G-G00292252!).

Description. Thallus foliicolous supracuticular, 7–20 mm across and 7–10 μm thick, smooth, pale grey. Photobiont *Phycopeltis*, cells rectangular, $5-14 \times 3-5 \mu\text{m}$, forming slightly radiating networks with interspaces. Perithecia erumpent and typically covered by a distinct thallus layer up to ostiole, wart-shaped to conical, $0.2-0.4$ mm diam. and $80-110 \mu\text{m}$ high, black; excipulum prosoplectenchymatous, $7-15 \mu\text{m}$ thick, colorless to brown; involucrellum carbonized, $12-25 \mu\text{m}$ thick, black; paraphyses unbranched. Asci oblong, $32-53 \times 5-7 \mu\text{m}$. Ascospores biseriate, fusiform-ellipsoid, 1-septate, with slight constriction at septum, $7-13 \times 2-3 \mu\text{m}$, 3.5–4.5 times as long as broad. Pycnidia erumpent, covered by a distinct thallus layer, wart-shaped, those producing macroconidia $0.1-0.15$ mm, those producing microconidia rare, $0.07-0.1$ mm diam., dark grey to greyish black. Macroconidia bacillar, 1-septate, $9-11 \times 2-2.5 \mu\text{m}$. Microconidia fusiform-ellipsoid, non-septate, $3-5 \times 1.5-1.8 \mu\text{m}$.

Chemistry: No substances detected by TLC.

Distribution and ecology: *Phylloporis obducta* is a common, presumably pantropical species reported from Costa Rica, Panama, Columbia, Guiana, French Guiana, Ecuador, Brazil (including the type), Peru, the Philippines, and Australia, among other countries (Santesson 1952; Santesson and Tibell 1988; Lücking 2008). However, it is questionable whether this taxon constitutes a single species. Here reported for the first time from China.

Notes: *Phylloporis obducta* appears to be most closely related to *Phylloporis phyllogena*, from which it differs by smaller perithecia with a more rounded top, covered by a distinct, greenish to grey thallus layer (Lücking 2008). The

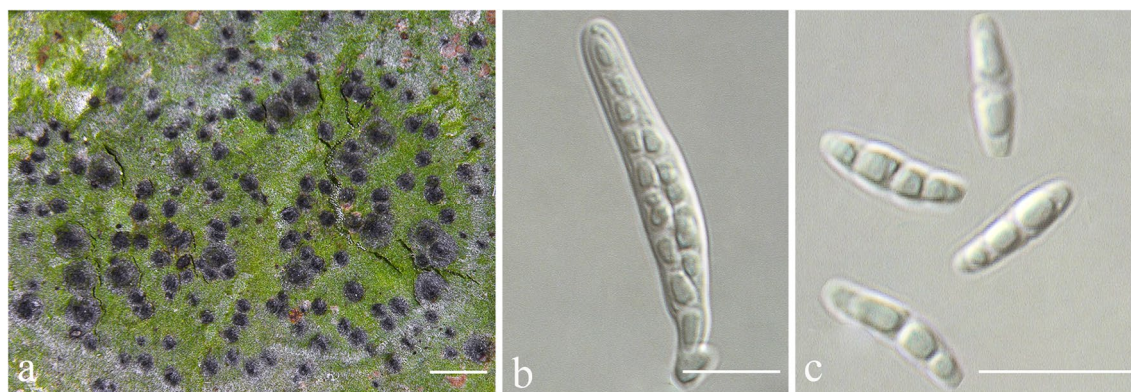


Fig. 16 *Phylloporis* cf. *obducta*. **a** Thallus (HMAS-L0139224), **b** Asci (HMAS-L0139237), **c** Ascospores (HMAS-L0139237). Scale bars: **a** = 300 μm , **b**, **c** = 10 μm

identification of the sequenced Chinese material is preliminary; it differs in a rather thin covering thallus layer of the perithecia and the somewhat radiating arrangement of the perithecia, somewhat similar to *P. vulgaris* (Lücking 2008).

Additional specimens examined. CHINA. Guangxi: Longzhou County, Nonggang National Nature Reserve; 22° 27' 55" N, 106° 57' 5" E, 270 m; on living leaves; 3 December 2015, S.H. Jiang GX201511203 (HMAS-L0139220), GX201511214 (HMAS-L0139224), GX201511217 (HMAS-L0139226), GX201511219 (HMAS-L0139218), GX201511222 (HMAS-L0139280), GX201511224 (HMAS-L0139281), GX201511302_3 (HMAS-L0141663), GX201511302_4 (HMAS-L0141664), GX201511233 (HMAS-L0139228), GX201511265_4 (HMAS-L0141658), GX201511272 (HMAS-L0139236), GX201511274 (HMAS-L0139237), GX201511302 (HMAS-L0139324), GX201511302_2 (HMAS-L0141662), GX201511308 (HMAS-L0139222), GX201511308_2 (HMAS-L0141665), GX201511309 (HMAS-L0139283), GX201511310 (HMAS-L0139282), GX201511311 (HMAS-L0139286), GX201511312 (HMAS-L0139284), GX201511315 (HMAS-L0139246), GX201511316 (HMAS-L0139247), GX201511317 (HMAS-L0139248), GX201511320 (HMAS-L0139251), GX201511329 (HMAS-L0139285). Hainan: Changjiang County, Bawangling National Nature Reserve; 19° 07' 07" N, 109° 09' 12" E, 700 m; on living leaves; 4 September 2017, S.H. Jiang HN20171702 (HMAS-L0139635). Yunnan: Xishuangbanna, Mengla County, tropical botanical garden of Chinese Academy of Sciences, East area; 21° 55' 39" N, 101° 15' 52" E, 560 m; on living leaves; 18 November 2015, X.L. Wei & S.H. Jiang XTBG2015039 (HMAS-L0139351), XTBG2015039_2 (HMAS-L0141538), XTBG2015042_1 (HMAS-L0141574), XTBG2015045 (HMAS-L0139352), XTBG2015046 (HMAS-L0139357), XTBG2015046_2 (HMAS-L0141575), XTBG2015082 (HMAS-L0139377), XTBG2015087 (HMAS-L0139338), XTBG2015093 (HMAS-L0139339). AUSTRALIA. Queensland: Josephine Falls, Wooroonooran National Park, 20 km NW of Innisfail; 17°26'16" S, 145° 51' 33" E, 80 m; on leaves of trees in lowland, tropical rainforest; 31 July 2006, J.A. Elix 38767 (CANB).

Phylloporis radiata (Lücking) S.H. Jiang, Lücking & J.C. Wei, **comb. nov.**

Mycobank: MB 833572

Basionym: *Strigula radiata* Lücking, Fl. Neotrop. Monogr. 103: 224 (2008).

Phylloporis vulgaris (Müll. Arg.) S.H. Jiang, Lücking & J.C. Wei, **comb. nov.**

Mycobank: MB 833574

Basionym: *Haplopyrenula vulgaris* Müll. Arg., Flora 66: 273 (1883); *Strigula vulgaris* (Müll. Arg.) Lücking, Fl.

Neotrop. Monogr. 103: 221 (2008) [comb. inval., ICN Art. 41.5].

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Author contributions SHJ, JCW, and RL conceived and designed the study. SHJ collected material in China and ABX-L, MESC, AA, RL, and CVP provided specimens from Brazil, Cuba and Guatemala. S.H. Jiang generated the DNA sequence data and SHJ and RL performed the phenotypic assessment of the material. SHJ and RL analysed the data. SHJ, RL, and JCW wrote the manuscript draft and all authors revised the draft and approved the final manuscript.

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