Reallocation of foliicolous species of the genus *Strigula* into six genera (lichened *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 confluentus* 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  *Cephalocarpus* · 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 Strigulales) 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 comparative 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 Vézda (1984) restricted the family to three genera, Strigula, Phylloporis and Raciborskiella, a classification followed in some other works (e.g. Llarens 2003). Species assigned to Raciborskiella grow exclusively on the leaf underside, whereas species assigned to Phylloporis (and previously to Porina) are supra-cuticular (Santesson 1952; Vézda 1984). The subcuticular foliicolous species classified in Raciborskiella and Strigula thereby associate with photobionts in the genus Cephaluros (Trentepohliaceae), a semiparasitic alga which obtains carbohydrates through photosynthesis but other nutrients from the host leaves (Nelson 2008; Brooks et al. 2015). While Cephaluros appears to represent a phylogenetically coherent entity, it is nested within a broadly defined genus Trentepohlia s.lat. whose generic delimitation remains unresolved (Nelson 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, Phyllobatheliumae (Eriksson et al. 2004; Eriksson 2005). Molecular data (Nelsen et al. 2009) supported the inclusion of Phyllobatheliumae 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, Tenuitholiaccaeae, sister to Strigulaceae in Strigulales (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, nuL SU) 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 *Strigulas* 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 Funarium-Lichenarium of the Institute of Microbiology, Chinese Academy of Sciences (HMAS-L), the herbarium of the Botanischer Garten und Botanisches Museum and 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 Havanna (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 *Strigulas*-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 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 μl reaction volume and the components used were 2 μl total DNA, 1 μl each primer (10 μM), 12.5 μl 2× Taq MasterMix, 8.5 μl 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 (Katoh 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, and the TEF1-α gene regions.

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

| Primer acronym | Primer sequence   |
|---------------|-------------------|
| SR3           | GCTGCGTTCTTCATCGTTGC |
| LR71          | TACTACCACCAAGATCTGC |
| 28SR4R        | TTTTCGGACCTCTAGGCTC |
| 28BYF1        | ATGAAAGAACGGCGAATAATG |
| NEWR2         | CTAACCCAGCTCACGTGTC |

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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 | RPB2 |
|--------------------------------|-------------|---------|----------------------|-------|-------|-------|--------|------|
| *Flavobathelium epiphyllum*    | MPN-67      |         |                      | –     | –     | –     | –      | –    |
| *Phyllobathelium anomalum*     | MPN-242     |         |                      | –     | –     | –     | –      | –    |
| *Phylloporis* cf. *obducta*    | HMAS-L0139218 | China   | S.H. Jiang           | –     | MN720034 | MN727002 | MN738504 | MN738529 |
| *Phylloporis* cf. *obducta*    | HMAS-L0139247 | China   | S.H. Jiang           | –     | MN720035 | MN727003 | MN738505 | MN738530 |
| *Phylloporis* cf. *obducta*    | HMAS-L0139286 | China   | S.H. Jiang           | –     | MN720036 | MN727004 | MN738506 | MN738531 |
| *Phylloporis* cf. *obducta*    | HMAS-L0139339 | China   | X.L. Wei & S.H. Jiang| –     | MN720037 | MN727005 | MN738507 | MN738532 |
| *Phylloporis* cf. *obducta*    | HMAS-L0139635 | China   | S.H. Jiang           | –     | MN720038 | MN727006 | MN738508 | MN738533 |
| *Phylloporis phyllogena*       | ISE-33944   | Brazil  | A. B. Xavier Leite   | –     | MN720039 | MN727007 | MN738509 | MN738534 |
| *Puiggariella nemathora*       | ISE-32586   | Brazil  | A. B. Xavier Leite   | –     | –     | –     | MN727009 | MN738510 |
| *Puiggariella nemathora*       | ISE-32794   | Brazil  | A. B. Xavier Leite   | –     | –     | –     | MN727008 | MN738535 |
| *Puiggariella nigro-cincta*    | HMAS-L0139335 | China   | X.L. Wei & S.H. Jiang| –     | MN720040 | MN727010 | MN738511 | MN738536 |
| *Puiggariella nigro-cincta*    | HMAS-L0139350 | China   | X.L. Wei & S.H. Jiang| –     | MN720041 | MN727011 | MN738512 | MN738537 |
| *Puiggariella nigro-cincta*    | HMAS-L0141541 | China   | X.L. Wei & S.H. Jiang| –     | MN720042 | MN727012 | MN738513 | MN738538 |
| *Raciborskiella janie-rensis* | HMAS-L0130589 | China   | J.H. Wang & R.D. Liu| –     | MN720043 | MN727013 | MN738514 |
| *Raciborskiella talaumae*      | HMAS-L0139624 | China   | S.H. Jiang           | –     | MN720044 | MN727014 | MN738515 |
| *Raciborskiella talaumae*      | HMAS-L0139627 | China   | S.H. Jiang           | –     | MN720045 | MN727015 | MN738516 |
| *Racoplaca melanobapha*         | HMAS-L0139331 | China   | X.L. Wei & J.H. Wang  | –     | MN720046 | MN727016 | MN738517 | MN738539 |
| *Racoplaca melanobapha*         | HMAS-L0139623 | China   | S.H. Jiang           | –     | MN720047 | MN727017 | MN738518 | MN738540 |
| *Racoplaca subtilissima*        | ISE-32602   | Brazil  | A. B. Xavier Leite   | –     | –     | –     | MN727018 | MN738519 |
| *Serusiauxiella filifera* sp. nov. | HMAS-L0130625 | China   | J.H. Wang & R.D. Liu| MN720009 | –     | –     | –      | –    |
| *Serusiauxiella filifera* sp. nov. | HMAS-L0130627 | China   | J.H. Wang & R.D. Liu| MN720010 | –     | –     | –      | –    |
| *Serusiauxiella filifera* sp. nov. | HMAS-L0130629 | China   | J.H. Wang & R.D. Liu| MN720011 | MN720048 | MN727019 | MN738520 | MN738541 |
| *Serusiauxiella filifera* sp. nov. | HMAS-L0139219 | China   | S.H. Jiang           | MN720019 | –     | –     | –      | –    |
| *Serusiauxiella filifera* sp. nov. | HMAS-L0139223 | China   | S.H. Jiang           | MN720020 | –     | –     | –      | –    |
| *Serusiauxiella filifera* sp. nov. | HMAS-L0139234 | China   | S.H. Jiang           | MN720022 | –     | –     | –      | –    |
| *Serusiauxiella filifera* sp. nov. | HMAS-L0139270 | China   | X.L. Wei & J.H. Wang  | MN720012 | –     | –     | –      | –    |
| *Serusiauxiella filifera* 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 | RPB2       |
|--------------------------|-------------|-----------|---------------------|-----------|-------|-------|--------|------------|
| *Serusiauxiella filifera* sp. nov. | HMAS-L0139288 China S.H. Jiang | MN720021 | – | – | – |
| *Serusiauxiella filifera* sp. nov. | HMAS-L0139298 China S.H. Jiang | MN720015 | – | – | – |
| *Serusiauxiella filifera* sp. nov. | HMAS-L0141639 China S.H. Jiang | MN720014 | – | – | – |
| *Serusiauxiella filifera* sp. nov. | HMAS-L0141641 China S.H. Jiang | MN720016 | – | – | – |
| *Serusiauxiella filifera* sp. nov. | HMAS-L0141644 China S.H. Jiang | MN720017 | – | – | – |
| *Serusiauxiella filifera* sp. nov. | HMAS-L0141648 China S.H. Jiang | MN720018 | MN720049 | MN720720 | MN738521 | MN738542 |
| *Serusiauxiella filifera* sp. nov. | HMAS-L0141656 China S.H. Jiang | MN720023 | MN720050 | MN720721 | MN738522 | MN738543 |
| *Serusiauxiella filifera* sp. nov. | HMAS-L0141660 China S.H. Jiang | MN720024 | – | – | – |
| *Serusiauxiella flagellata* sp. nov. | HMAS-L0130554 China J.H. Wang & R.D. Liu | MN720025 | – | – | – |
| *Serusiauxiella flagellata* sp. nov. | HMAS-L0141609 China J.H. Wang & R.D. Liu | MN720026 | – | – | – |
| *Serusiauxiella flagellata* sp. nov. | HMAS-L0139216 China J.H. Wang & R.D. Liu | MN720027 | – | – | – |
| *Serusiauxiella sinensis* sp. nov. | HMAS-L0141605 China J.H. Wang & R.D. Liu | MN720033 | – | – | – |
| *Serusiauxiella sinensis* sp. nov. | HMAS-L0141611 China J.H. Wang & R.D. Liu | MN720031 | MN720053 | MN720722 | MN738525 | MN738546 |
| *Serusiauxiella sinensis* sp. nov. | HMAS-L0141612 China J.H. Wang & R.D. Liu | MN720032 | – | – | – |
| *Serusiauxiella sinensis* sp. nov. | HMAS-L0141614 China J.H. Wang & R.D. Liu | MN720030 | – | – | – |
| *Strigula acuticonidiarum* | HMAS-L0138045 – | MK206236 | MK206217 | MK273083 | MK273111 |
| *Strigula antillarum* | B-600205084 Cuba R. Lücking et al. | – | MN720054 | – | MN738526 | MN738547 |
| *Strigula cf. atrocarpoides* | HMAS-L0139342 China X.L. Wei & S.H. Jiang | – | MN720055 | MN720723 | MN738527 | MN738548 |
| *Strigula dispersa* | HMAS-L0137212 – | – | MN720056 | – | MK273097 | MK273125 |
| *Strigula guangxiensis* | HMAS-L0138040 – | – | MK206256 | – | MK273103 | MK273131 |
| *Strigula guangxiensis* | HMAS-L0138041 – | MK206257 | – | MK273104 | MK273132 |
| *Strigula jamesii* | MPN-548 – | JN887404 | JN887388 | JN887432 – |
| *Strigula cf. macaronenesica* | HMAS-L0130615 – | MK206251 | MK206230 | MK273098 | MK273126 |
| *Strigula cf. macaronenesica* | HMAS-L0139260 – | MK206252 | MK206231 | MK273099 | MK273127 |
| *Strigula macrocarpa* | HMAS-L0139289 – | MK206241 | MK206222 | MK273088 | MK273116 |
| *Strigula macrocarpa* | HMAS-L0141394 – | MK206240 | MK206221 | MK273087 | MK273115 |
| *Strigula nitidula* | HMAS-L0139358 – | MN788374 | MN788375 | MN793983 | MN793982 |
| *Strigula prasina* | B-600205026 Guatemala R. Lücking et al. | – | – | MN727024 | MN738528 – |
| *Strigula sinoaustralis* | HMAS-L0137204 – | MK206249 | – | MK273096 | MK273124 |
| *Strigula smaragdula* | HMAS-L0138066 – | KY100296 | – | – | – |
| *Strigula smaragdula* | HMAS-L0138068 – | KY100299 | – | – | – |
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.

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/phylows/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 2 (continued)

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

Newly generated sequences are indicated in boldface.
Table 3 GenBank accession numbers for other sequences used in the molecular phylogenetic analyses

| Species                          | LSU    | SSU    | TEF1-α | RPB2  |
|---------------------------------|--------|--------|--------|-------|
| Acrospermum adeanum             | EU940104 | EU940031 | –      | EU940320 |
| Acrospermum compressum          | EU940084 | EU940012 | –      | EU940301 |
| Acrospermum gramineum           | EU940085 | EU940013 | –      | EU940302 |
| Aigialus grandis                | GU301793 | GU296131 | –      | GU371762 |
| Aigialus parvus                 | GU301795 | GU296133 | GU349064 | GU371771 |
| Aliquandostipite khaoyaiensis   | GU301796 | AF201453 | GU349048 | FJ238360 |
| Anisomeridium ubianum           | GU327709 | JN887379 | –      | –     |
| Apiospora collinsii             | GU301798 | GU296135 | –      | EU940357 |
| Aquasubmersa japonica           | LC061588 | LC061583 | LC194385 | LC194422 |
| Arthopyrenia salicis            | AY538339 | AY538333 | –      | –     |
| Ascocratera manglicola          | GU301799 | GU296136 | –      | GU371763 |
| Asterina cestrica               | GU586215 | GU586209 | –      | –     |
| Asterina fuchsiae               | GU586216 | GU586210 | –      | –     |
| Asterina phenacis               | GU586217 | GU586211 | –      | –     |
| Asterina weinnanniae            | GU586218 | GU586212 | –      | –     |
| Asterina zanthoxyli             | GU586219 | GU586213 | –      | –     |
| Aureobasidium pullulans         | DQ470956 | DQ471004 | DQ471075 | DQ470906 |
| Botryobambusa fusiscoccum       | JX646809 | JX646826 | –      | –     |
| Botryosphaeria agaves           | JX646808 | JX646825 | –      | –     |
| Botryosphaeria dothidea         | DQ678051 | DQ677998 | DQ767637 | DQ677944 |
| Delitschia didyma               | DQ384090 | AF242264 | –      | –     |
| Delitschia winteri              | DQ678077 | DQ678026 | DQ767922 | DQ677975 |
| Dendrographa decolorans         | AY548815 | AY548809 | DQ883725 | DQ883715 |
| Dothidea hippophaeos            | DQ678048 | U42475  | DQ677887 | DQ677942 |
| Dothidea insculpta              | DQ247802 | DQ247810 | DQ471081 | AF107800 |
| Dothidea sambuci                | AY544681 | AY544722 | DQ479606 | KT216559 |
| Dothiora cannabisae             | DQ470984 | DQ479933 | DQ471107 | DQ470936 |
| Dyfrolomyces rhizophorae        | GU479799 | GU479766 | GU479860 | –     |
| Dyfrolomyces tiomanensis        | KC692156 | KC692155 | KC692157 | –     |
| Elsinoe centrolobi              | DQ678094 | DQ678041 | DQ677934 | –     |
| Elsinoe phaseoli                | DQ678095 | DQ678042 | DQ677935 | –     |
| Elsinoe veneta                  | DQ767658 | DQ767651 | DQ767641 | –     |
| Falciiformispora lignatilis     | GU371826 | GU371834 | GU371819 | –     |
| Fal. senegalensis               | KF015627 | KF015634 | KF015688 | KF015716 |
| Fal. tompkinsii                 | KF015625 | KF015640 | KF015685 | KF015716 |
| Gibbera conferta                | GU301814 | GU296150 | GU349046 | –     |
| Gloiopsis praelonga             | FI161195 | FI161154 | FI161103 | FI161113 |
| Glonium circumserpens           | FI161200 | FI161160 | FI161108 | FI161126 |
| Glonium stellatum               | FI161179 | FI161140 | FI161095 | –     |
| Hysteropatella clavispora       | AY541493 | DQ678006 | DQ677901 | DQ677955 |
| Jahnula aquatica                | EF175655 | EF175633 | –      | –     |
| Jahnula bipileata               | EF175657 | EF175635 | –      | –     |
| Kirschsteiniothelia aethiops    | AY016361 | AY016344 | DQ767884 | DQ470914 |
| Kirschsteiniothelia lignicola   | HQ441568 | HQ441569 | –      | –     |
| Lecanactis abietina             | AY548812 | AY548805 | DQ987635 | –     |
| Lepidosphaeria nicotiae         | DQ678067 | DQ677910 | DQ677963 | –     |
| Lichenolconium aeruginosum      | HQ174269 | –      | –      | –     |
| Lichenolconium erodens          | HQ174267 | –      | –      | –     |
| Lichenolconium lecanorae        | HQ174263 | –      | –      | –     |
| Lichenolconium asneae           | HQ174265 | –      | –      | –     |
| Lichenothelia calcarea          | KC015061 | KC015081 | –      | –     |
conflict in the nuSSU with the nuLSU and the concatenated data set. The Serusiauxiella 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 sub-clades 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
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 Teniotholiascaceae (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 Teniotholiascaceae 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 perithcal 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 a 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 4 Voucher information and GenBank accession numbers for specimens of used for the molecular phylogenetic analyses of Trentepohliaceae photobionts

| Species                                                                 | DNA extract   | ITS             |
|------------------------------------------------------------------------|---------------|-----------------|
| Cephalaeuros expansus                                                  | GD1318        | KX586811        |
| Cephalaeuros karstenii                                                 | DZ1309        | KX586781        |
| Cephalaeuros karstenii                                                 | DZ1312        | KX586784        |
| Cephalaeuros sp. from Strigula sp.                                     | HMAS–L0130622 | MK211171        |
| Cephalaeuros sp. from Strigula cf. smaragdula                          | HMAS–L0141395 | MK211172        |
| Phycopeltis aurea                                                      | YN1220 (IHB)  | KP067280        |
| Phycopeltis prostrata                                                  | YN1218 (IHB)  | KP067283        |
| Phycopeltis sp. from Teniotholiascus porinoides                        | HMAS–L0139638 | MK211174        |
| Phycopeltis sp. from Teniotholiascus porinoides                        | HMAS–L0141346 | MK211173        |
| Phycopeltis sp. from Phylloporis cf. obducta                           | HMAS–L0139220 | MN718160        |
| Phycopeltis sp. from Phylloporis cf. obducta                           | HMAS–L0139228 | MN718161        |
| Phycopeltis sp.                                                        | YN1202        | KP067279        |
| Trentepohlia sp. from Serusiauxiella filifera sp. nov.                 | HMAS–L0130629 | MN718162        |
| Trentepohlia sp. from Serusiauxiella flagellata sp. nov.               | HMAS–L0139216 | MN718163        |
| Trentepohlia sp. from Serusiauxiella flagellata sp. nov.               | HMAS–L0130554 | MN718164        |
| Trentepohlia sp. from Serusiauxiella sinensis sp. nov.                 | HMAS–L0141614 | MN718165        |
| Trentepohlia sp.                                                        | DS22          | KC489115        |
| Trentepohlia sp.                                                        | SAG118.80     | KM020078        |
| Trentepohlia sp.                                                        | TrefFl54      | KC489121        |
| Ulva tepida                                                            | PR18          | KT374011        |

Newly generated sequences are indicated in boldface.
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 | RPB2 | Concatenated |
|---------|---------|------|------|--------|------|--------------|
| Phylloporis | 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%) |
| Puiggariella | 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%) |
| Raciborskiella | 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%) |
| Racoplaca | Topology | Mono, SB (100%) | Mono, LB (100%) | Mono, LB (100%) | Mono, LB (100%) | SISTER to Pui + S. prasina (95%) |
|          | Position | Sister to Pui (92%) | Sister to Pui (92%) | Sister to Pui (unsupported) | Sister to Pui + Ser (unsupported) | Sister to Pui + S. prasina (95%) |
| Serusiauxiella | Topology | Mono, LB (100%) | Mono, LB (100%) | Mono, LB (100%) | Mono, LB (100%) | Mono, LB (100%) |
|          | Position | Sister to Rpl + S. prasina clade (unsupported) | Sister to Rac (94%) | Sister to Ser + Str core (70%) | Sister to Pui (73%) | Sister to Rac (98%) |
| Strigula s.str. | Topology | Mono, SB (100%) (except S. prasina clade) | Paraphyletic (unsupported) | Poly, SB (unsupported) | Mono, SB (98%) | Mono, SB (95%) |
|          | Position | Sister to Rpl + Ser + S. prasina clade (80%) | MOSTLY basal to Phy + Rac + Ser; S. prasina and S. nitidula clades separate from core (unsupported) | Core sister to Ser (70%); S. nitidula and S. prasina 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 Tenuithioliascaceae (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 macroconidia, 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 macronidial 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 markers (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*.
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 μm or more. In contrast, in all species of *Serusiauxiella*, the appendages extended to up to 70 μm 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.
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 supra-cuticularly 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 thallus 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...
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 × 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. 4 Synoptic phylogenetic tree of Strigulaceae showing mapped phenotype features. The asterisk* indicates original photobiont drawings by Lücking (1992)](image-url)
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 Santeesson (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 redispersioned 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...
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 \textit{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
2. Perithecia immersed in thalline verrucae, aggregated in pseudostromata filled with ochraceous-yellow, K + red crystals; paraphyses rather thick (1.5–2 μm); pycnidia aggregate in pseudostromata similar to those of perithecia; macroconidia acicular, 3–5-septate, one end with gelatinous appendages, the other with gelatinous cap.......................... [\textit{Flavobathelium}]

3. Perithecial wall not carbonized; thallus subcuticular, with numerous minute, white papillae

4. Thallus supracuticular, easily separated from the leaf surface; photobiont \textit{Phycopeltis} (forming radiating or reticulate plates of rectangular cells) ............ \textit{6. Phylloporis}

5. Thallus subcuticular, more difficult to separate from the leaf surface; photobiont \textit{Cephaleuros} or \textit{Trentepohlia} (forming one or several layers of irregular groups or threads of angular-rounded cells) .........................

6. Ascospores large (30–70 μm long); thallus thin, typically dark bluish grey, always hypophyllous.......................... \textit{3. Raciborskiella}

7. Ascospores small to medium-sized (7–25 μm); thallus thin to thickened, usually bright to dark green to grey-green or olive-brown, usually epiphyllous, rarely bluish grey and/or hypophyllous .................................

8. 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 ostiolar, therefore not pure black ............ \textit{5. Racoplaca}

9. Thallus bright green to grey-green or rarely with bluish tinge, with entire to crenulate or lobed margin but
rarely laciniate, 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 *Cephaleuros*…………………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, pulvinate 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………………*[Phylloclerata]*

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 perithelial 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-L0141634), GX2016005_5 (HMAS-L0141635), GX2016005_6 (HMAS-L0141637), GX2016006 (HMAS-L0139209), GX2016006_2 (HMAS-L0141634), GX2016006_3 (HMAS-L0141635), GX2016007 (HMAS-L0139210). Shangsi County, Shiwan
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 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.

**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*

2. 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 ends. .......................... *Serusiauxiella flagellata*

2. Asci 40–65 μm long .......................... *Serusiauxiella sinensis*

2. Asci 50–80 μm long .......................... *Serusiauxiella flagellata*

2. Asci 40–65 μm long .......................... *Serusiauxiella sinensis*
Additional specimens examined. CHINA. Guangxi: Nanjing, 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).

Fig. 8  *Serusiauxiella filifera* sp. nov. (holotype, HMAS-L0130626)  

a Thallus, b Asci, c, d Ascospores, e Macroconidia with extremely long appendages. Scale bars: a = 600 μm, b–e = 10 μm
Serusiauxiella flagellata S.H. Jiang, Lücking & J.C. Wei, sp. nov.  

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-L0130554).

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] C-G (314), C-T (17, 78, 87, 92, 105, 349); [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 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 biseriate or irregularly arranged, 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 HN20142420_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.  

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 biseriate 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 producing macroconidia immersed-erumpent, wart-shaped, 0.1–0.15 mm, black; 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.
Notes: This new species is very similar to *Serusiauxiella 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-L0139216); 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, hypophylous, 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, biseriate to irregular arranged, fusiform, 1-septate, colorless, rather large,
30–70 × 5–7 μm, 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 μm 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. s., ascospore appendages have so far only been reported from one species currently placed in Strigula s. s., ascospore appendages are absent in many species of Strigula s. s. 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).

*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 foliicolous, subcuticular, with entire margins or crenulate lobulate to lobulate, 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; hamatheicum colorless, I–, KI–; paraphyses unbranched, thin. Asci bitunicate, with short tholus and narrow, ocular chamber, I–; clamp connections absent.

**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 noted 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, Xitianping 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 apiayhyna Speg. [= Puiggariella nemathora (Mont.) S.H. Jiang, Lücking & J.C. Wei].

**Description**: Thallus foliicolous, subcuticular, with entire margins or crenulate lobulate to lobulate, 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; hamatheicum colorless, I–, KI–; paraphyses unbranched, thin. Asci bitunicate, with short tholus and narrow, ocular chamber, I–; clamp connections absent. Ascospores 8 per ascus, uniseriate to biseriate, fusiform, 1-septate, colorless, 15–25 × 4–6 μm. Pycnidia immersed-erumpent, wart-shaped to conical, pale to brownish. Microconidia bacilar 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 laciniate 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.
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 laciniate and in part leaving interspaces, irregular to regularly radiating; lobe margins with numerous, minute papillae .............

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.  

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

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Fig. 12  

*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. Ascii 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.**

*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 laciniate, 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 × 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...
prosoplectenchymatous, 12–25 μm thick, colorless; involucrellum confluent with excipulum, 30–70 μm thick, colorless to pale brown; paraphyses unbranched. Asci oblong, 80–110 × 7–10 μm. Ascospores uniseriate to irregularly arranged, 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: 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.  
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 laciniate, 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 biseriate, 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 thallus. 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
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-L0139366), XTBG2015050_1
(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_2 (HMAS-L0141557),
XTBG2015066_3 (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-L0141569), XTBG2015075_2
(HMAS-L0139374), XTBG2015076 (HMAS-L0141570),
XTBG2015118 (HMAS-L0141537). 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): lxviii, xciv,
xcix (1825) [1824].

**Type species.** *Racoplaca subtilissima* Fée.

**Description:** Thallus folicolous, crustose, subcortical,
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, biseriate
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
pheno-typically distinctive. Besides the type species, the genus
includes four further taxa.

**Key to species of *Racoplaca***

1. **Ascospores** fusiform, 14–23 × 3–5 μm
   ………………………………………………………………………………………………………………………………………………………… 2
   1. Ascospores oblong, 8–18 × 2–3 μm ……………………………3
   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*
   4. Laciniae thickened, with conspicuous transverse undula-
ations …………………… *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.**

*MycoBank*: MB 833586

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

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

**Description**: Thallus subcuticular, typically laciniate, 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 biseriate, 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...
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 GD20150663 (HMAS-L0141593); ibid.; 24° 56’ 59" N, 112° 56’ 02" E, 1257 m; on living leaves; 26 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). Mossman Gorge, Daintree National Park, 6 km W of Mossman; H. Streimann 61677 p.p. (CANB).

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

MycoBank: MB 833589

Basionym: *Strigula transversouludata* 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 02003461).

**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: Apiayha; 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, supra- and subcuticular, 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 prosoplectenchymatous, 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, biseriate 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 supra- and subcuticular 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
2. Thallus lacking black dots; ascospores remaining entire .......................................................... 3
2. Ascospores 12–16 × 3.5–4.5 μm ............................... Phylloporis multipunctata
3. Ascospores 20–30 × 4–6 μm ................................. Phylloporis multipunctata
4. Photobiont cells forming contiguous, regularly radiating plates ........................................ Phylloporis vulgaris
5. Photobiont cells forming irregular to somewhat radiating networks with interspaces ................................. Phylloporis viridis
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 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. .............................................................. Phylloporis obducta
4. Perithecia exposed or covered by thin thallus layer, black to greyish black, conical, 0.3–0.5 mm diam. .................................................. Phylloporis phyllogena
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 Phylloporis cf. obducta. a Thallus (HMAS-L0139224), b Asci (HMAS-L0139237), c Ascospores (HMAS-L0139237). Scale bars: a = 300 μm, b, c = 10 μm

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
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, Bangawangling National Nature Reserve; 19° 07′ 07″ N, 109° 09′ 12″ E, 700 m; on living leaves; 27 November 2015, L.C. Zeng GX201511304 (HMAS-L0139221), GX201511305 (HMAS-L0139223), GX201511307 (HMAS-L0139225), GX201511308 (HMAS-L0139227), GX201511309 (HMAS-L0139229), GX201511310 (HMAS-L0139280), GX201511311 (HMAS-L0139284), GX201511312 (HMAS-L0139285), GX201511315 (HMAS-L0139246), GX201511316 (HMAS-L0139247), GX201511317 (HMAS-L0139248), GX201511320 (HMAS-L0139251), GX201511329 (HMAS-L0139285). 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).

**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.
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