Foliicolous Lichens in the Black Forest, Southwest-Germany

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Abstract
We report the unexpected discovery of foliicolous lichen communities at several localities in the Black Forest, south-western Germany, with a total of seven truly or facultatively foliicolous taxa: *Bacidina chloroticula*, *Fellhanera bouteillei*, *F. subtilis*, *F. viridisorediata*, *Fellhaneropsis myrtillicola*, *Gyalectidium setiferum*, and *Scoliciosporum curvatum*. The communities are similar to those reported previously from Belgium, western Germany (Mosel valley), and Austria (Styria), apparently forming a characteristic association across central Europe (*Fellhaneretum myrtillicolae* Spier & Aptroot), but are richer in species in the Black Forest than in any of the other areas studied. An identification key is provided to the species of this association in the Black Forest. *Gyalectidium setiferum* is new for central Europe, and *Scoliciosporum curvatum* is new to southern Germany. Since these lichen communities appear to be confined to well-conserved forest and depend on favorable, warm-humid climatic conditions, their potential use as indicators of global climatic change is discussed.

Kurzfassung
Foliicole Flechten im Schwarzwald, Südwest-Deutschland
Im Schwarzwald wurden überraschenderweise an etlichen Lokalitäten foliicole Flechtenbestände mit insgesamt sieben bevorzugt oder häufig foliicolen Arten gefunden: *Bacidina chloroticula*, *Fellhanera bouteillei*, *F. subtilis*, *F. viridisorediata*, *Fellhaneropsis myrtillicola*, *Gyalectidium setiferum* und *Scoliciosporum curvatum*. Die Bestände sind ähnlich zusammengesetzt wie die zuvor von Belgien, Westdeutschland (Moseltal) und Österreich (Steiermark) nachgewiesenen; sie bilden eine offenbar charakteristische, in Zentraleuropa heimische Gesellschaft (*Fellhaneretum myrtillicolae* Spier & Aptroot), die aber im Schwarzwald reicher entwickelt und häufiger ist als in allen anderen untersuchten Gebieten. Ein Bestimmungsschlüssel für diese Arten ist eingefügt. *Gyalectidium setiferum* ist neu für Zentraleuropa, *Scoliciosporum curvatum* neu für Süddeutschland. Da das Vorkommen foliicoler Flechtengemeinschaften von der Erhaltung natürlicher Wälder und von klimatischen Bedingungen abhängt, wird die potenzielle Nutzung dieser Flechten als Bioindikatoren der globalen Klimaerwärmung kurz diskutiert.

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1 Introduction

Foliicolous lichens grow on the surface of living leaves of vascular plants (shrubs, trees, and epiphytes). Since leaves are ephemerous in nature, leaf-dwelling lichens have to complete their life cycle quickly (Lücking 2001, 2008). Studies in tropical climates show first traces of colonization on young leaves after about six months, and mature lichen thalli with reproductive organs develop after 24 to 36 months (Lücking & Bernecker-Lücking 2002, Sanders & Lücking 2002). Therefore, foliicolous lichen communities cannot develop on plants that shed their leaves annually, such as the trees that dominate in temperate and tropical dry deciduous forests. Since the thalli adhere to the leaf surface by means of a polysaccharid layer (mucilage), a high level of humidity is also required for foliicolous lichens to develop.
In temperate regions, not all trees and shrubs are deciduous, and those that have leaves with a longevity of more than one year can support foliicolous lichen communities under certain conditions. Besides conifers, specifically *Abies*, evergreen broad-leaved trees, shrubs, and lianas or climbers that could potentially support foliicolous lichens include *Ilex*, *Hedera*, *Buxus*, and planted *Rhododendron*. Mild and humid oceanic climate favors the development of foliicolous lichen communities. In Europe, such communities have been described primarily from the Mediterranean region and the temperate oceanic western and north-western parts of the continent (Sérusiaux 1993, Puntillo *et al.* 2000, Llop & Gómez-Bolea 2006). They usually consist of a mixture of truly foliicolous species such as *Gyalectidium* and *Strigula* spp., as well as taxa that are rather broad in their substrate choice, such as *Fellhanera bouteillei*. Other compo-

nents are usually corticolous taxa that grow well on leaves under certain circumstances (facultatively foliicolous), such as *Scoliciosporum* spp., and accidentally foliicolous thalli that usually do not reach maturity on leaves, including foliose macrolichens.

In central Europe, foliicolous lichen communities are rare and usually restricted to needles of conifers and mostly comprise substrate-indifferent and facultatively foliicolous species, including *Fellhanera bouteillei, F. subtilis*, and *Gyalideopsis piceicola*, as well as accidentally foliicolous taxa like *Hypogymnia tubulosa* and *Physcia tenella*. The few evergreen broad-leaved trees and shrubs occurring in the south-western Germany were not believed to support foliicolous lichens; for example, the *Buxus* forest near Grenzach, at the border between Germany and Switzerland, was searched in vain for leaf-dwelling lichen communities by Lettau (1940) and Wirth (1979). This is not unexpected as the climatic conditions in this south-facing forest are comparatively dry. Another problem for the potential occurrence of foliicolous lichens is acid precipitation, stressing central European forests during the 1970s and 1980s (Bartholmess 1989). As a consequence, the chances of discovering foliicolous lichens in central European forests were considered to be too low to provoke the desire to actually look for them (Poelt & Vězda 1992).

Against this background, the discovery of a foliicolous lichen community on *Abies* needles in Austria (Styria) by Poelt & Vězda (1992) was surprising. Foliicolous lichens found there included *Fellhanera bouteillei*, *F. buxi* (Vězda & Vivant) Vězda [a synonym of *Fellhaneropsis myrtillicola* (Erichs.) Sérus. & Coppins], *Bacidina aphiaca* (Müll. Arg.) Vězda (identification later corrected to *B. chloroticula*, Hafellner & Türk 2001), and the newly described *Bacidia gorgonea* (another synonym of *Fellhaneropsis myrtillicola*). Another unexpected discovery were the foliicolous lichen communities found in humid valleys in Belgium (van den Boom & Sérusiaux 1996) and in the Mosel valley in nearby Germany (Rheinland-Pfalz, Killmann et al. 2004), with *Fellhanera bouteillei*, *Bacidina chloroticula*, *Arthonia muscigena*, and *Fellhaneropsis myrtillicola* at both localities and *Fellhanera subtilis* in Belgium, though the mentioned *Arthonia* and *Bacidina* species are considered facultatively foliicolous (Killmann et al. 2004). Cezanne et al. (2008) mentioned *Fellhaneropsis myrtillicola* from *Picea* needles in the Odenwald, Germany.

The recent discovery of foliicolous lichen communities in humid valleys of the Black Forest support the surprising notion that such communities are more widespread in central Europe than previously expected. The initial discovery of *Fellhanera bouteillei* and *F. viridisorediata* on needles of *Abies* and leaves of *Ilex* and *Rhododendron* by M.A. led V.W. (and M.A.) to revisit the locality and search for foliicolous lichens in other humid areas of the Black Forest. This resulted in the documentation of a surprisingly rich assembly, including seven truly or facultatively foliicolous species, particularly on needles of *Abies* and with up to five species co-occuring on single branchlets.

2 The foliicolous lichens found in the Black Forest and their habitats

We define foliicolous lichens as species starting their development on leaves or needles, thereby excluding lichens that secondarily grow onto the foliage from the bark of branches. Foliicolous species were found during our survey on *Abies, Picea, Taxus, Ilex, Buxus*, *Rhododendron*, and *Laurocerasus*. The number of phorophytes is less compared to the phorophyte species that support foliicolous bryophytes in the northern Black Forest (Ahrens 2009). However, the latter are not foliicolous taxa in the strict sense but rather overgrow leaves and needles under favorable warm-humid conditions.

In this paper, we are not using the common terminology of obligately and facultatively foliicolous lichens as introduced by Santesson (1952), since this distinction is misleading and does not give the different types of substrate preferences justice (Sérusiaux 1989, Lücking 2008). Usually foliicolous lichens can often be found on comparable substrata, particularly the smooth bark of small branches or bamboo culms, so they are not obligately confined to leaves. A better classification (into four categories) is given by considering the substrate abundances: (1) Truly foliicolous lichens are usually found on leaves and rarely on other substrata (many species of the genus *Strigula*). (2) Substrate-indifferent or "ubiquitous" species are commonly found on different types of substrata including leaves (examples would be *Fellhanera bouteillei* or the tropical *Byssoloma leucoblepharum* and *Coccocarpia* spp.). (3) Facultatively foliicolous species usually grow on other substrata but under certain conditions grow on leaves, but then their thalli are usually less well-

developed (e.g., *Fellhanera subtilis*). (4) Accidentally foliicolous lichens either overgrow leaves and needles from the bark of adjacent branches (i.e., they do not start their development on the leaf surface) or they form small, immature thalli on leaves under particular conditions, such as leathery leaves of shrubs and treelets in tropical high mountain areas (Lücking 2008); most foliose and fruticose macrolichens fall under this category. Only the first three categories are "self-sufficient", which means foliicolous communities can develop without the input from other substrata, because the species are able to complete their life cycles entirely on leaves or needles.

All seven lichen species discussed in detail below are foliicolous species initiating their thalli on the needles or leaves. Accidentally foliicolous species are not explicitedly discussed but have been listed following the species discussions and the key, for sake of completeness. In discussing the occurrence of truly, facultatively, and accidentally foliicolous lichens on different phorophytes, we use the term branches for all ramifications from the main trunk of the phorophyte, whereas the term "branchlets" refers to the terminal branches of fir and spruce on which the needles are concentrated. A single branchlet contains needles of a single year.

Bacidina chloroticula (Nyl.) Vězda & Poelt
(Plate 1A-B)

Bacidina chloroticula is considered a substrate-indifferent lichen as it has frequently been reported from other substrata across Europe; however, in the study area it makes the impression of being truly foliicolous as it is much more abundant on leaves and needles. The species was found at ten localities, generally on *Abies* needles and rarely also on *Rhododendron* and *Buxus* leaves. At one locality, *B. chloroticula* occurred throughout a valley of 1 km length. *Fellhanera bouteillei* usually co-occurred on the same trees, but only rarely on the same branchlets and needles as *B. chloroticula*. Furthermore, *Fellhaneropsis myrtillicola* was often associated with *B. chloroticula*. *Bacidina chloroticula* prefers shaded areas. According to our observations on fir branchlets representing subsequent years (chronosequences), the species usually develops its thallus on three-year old needles and produces apothecia on four-year old ones. The species is relatively indifferent with regard to its substrate and also grows on rock and wood, particularly tree stumps. From conifer needles, *B. chloroticula* was already reported by van den Boom & Sérusiaux (1996) and Killmann et al. (2004).The record of *Bacidina apiahica* from Austria by Poelt & Vězda (1992) also represents *B. chloroticula* (Hafellner & Türk 2001). These species are superficially similar, but *Bacidina apiahica* has larger, often more vividly colored apothecia than *B. chloroticula*. Moreover, the ascospores are twisted in the asci of *B. chloroticula*. The high abundance of *B. chloroticula* on fir needles suggests that they provide its quantitatively most important substrate in the study area. *Bacidina chloroticula* is probably the most shade-tolerant species among the foliicolous lichens found in the Black Forest. In addition, the species extends to higher elevations of the montane zone than the other foliicolous lichens. *Bacidina chloroticula* is apparently widespread in the Black Forest at sites with humid microclimate.

Germany, Baden-Württemberg. Northern Black Forest: Baden-Baden, Geroldsau, below Geroldsauer water fall, 280-300 m, on *Rhododendron*; 27.6.2009, Wirth 41166.; ibid.; 29.6.2009, Wirth & Ahrens 411167. Central Black Forest: Lahr, Sulz, Sulzbachtal, along forest trail on left side of valley, 210 m; 29.7.2009, Wirth & Ahrens 41261, 41269; ibid., 340 m; 29.7.2009, Wirth & Ahrens 41307 Alpirsbach, Aischbachtal, fir-spruce forest above water purification plant, 550 m; 16.8.2009, Wirth 41281. Southern Black Forest: Breitnau, Höllsteig, Ravennaschlucht, 720-740 m, on *Abies*; 9.9.2009, Wirth 41328. St. Ulrich, Aubach, fir plantation, 510 m, on *Abies*; 9.9.2009, Wirth 41327. Sulzburg, Bad Sulzburg, 440 m, on *Buxus*; 9.9.2009, Wirth 41329.

Fellhanera bouteillei (Desm.) Vězda
(Plate 1C-D)

Fellhanera bouteillei has long since been considered the most common foliicolous species in Germany (Wirth 1995, and unpubl. data; Killmann et al. 2004). This is also true for the Black Forest, although the species cannot longer be regarded as the only foliicolous lichen in this area and locally, other species (especially *Fellhaneropsis myrtillicola*) are more abundant. *Fellhanera bouteillei* is a substrate-indifferent species also growing on rock and the bark of branches and trunks. It is most common on conifer needles (*Abies*, rarer *Picea*, exceptional *Taxus* [near Geroldsau]), but also occurs on the leaves of *Buxus*, *Rhododendron*, and *Ilex*. On conifers, *F. bouteillei* is, like *Bacidina chloroticula*, richly fertile on four-year old needles, though a few apothecia are already

found on three-year old needles. White pycnidia with wide ostiole, which are characteristic of *F. bouteillei*, often cover the entire thallus surface. In humid localities of sheltered valleys, the species is particularly common on the slopes facing the valley of the river Rhine.

Germany, Baden-Württemberg. Northern Black Forest: Baden-Baden, Geroldsau, below Geroldsauer water fall, 280-300 m, on *Rhododendron*; 27.6.2009, Wirth 41166. Marxzell, Brach Siegen east of Schielberg, 325-335 m, on *Abies*; Ahrens s.n. Central Black Forest: Alpirsbach, Aischbachtal, 550 m; 16.8.2009, Wirth 41280. Schiltach, Eulersbach, 400 m, on *Picea*; 16.8.2009, Wirth s.n. Ettenheim, Ettenheimmünster, valley of the Dörlinbacher Grundbächle, 275 m, on *Abies*; 29.7.2009, Wirth 41295. Bleichheim near Herbolzheim, 1 km E of Muckental, Bleiche Valley, forest margin near fish ponds, 270 m, 29.7.2009, Wirth & Ahrens 41255. Lahr, Sulz, Sulzbachtal, along forest trail, 280 m; 29.7.2009, Wirth & Ahrens 41257. Southern Black Forest: Brenden, Schwarzatal below Eichholz, Talgrund, 580 m; 17.8.2009, Wirth & Wirth 41285; ibid., Schwarzatal between Eichholz and Leinegg, bottom of valley, 550 m; 18.8.2009, Wirth & Wirth 41286. Sulzburg, Bad Sulzburg, below public bath, near bottom of valley on left side, 440 m; 23.4.2004, Wirth 39888, 39889, 24.7.2009, Wirth 41243.

Fellhanera subtilis (Vězda) Sérus. & Diederich (Plate. 1E-F)
This species is commonly found in higher regions of the Black Forest in foggy or humid locations on shoots of *Vaccinium*, more rarely on branches of *Abies* (Wirth 1995). Although it was found here on needles more often than on the bark of branches, the thalli were always small (much smaller than those usually found on *Vaccinium* shoots, for example), and hence we consider this species to be facultatively foliicolous rather than substrate-indifferent. Due to its small thalli, *F. subtilis* is easily overlooked, and it can also resemble poorly developed forms of *F. bouteillei* and *Bacidina chloroticula* on leaves. Anatomically it is well-characterized by the pale yellowish apothecia and 3-septate, ellipsoid ascospores.

Germany, Baden-Württemberg. Northern Black Forest: Baden-Baden, Geroldsau, below Geroldsauer water fall, 280-300 m; 29.6.2009, Wirth & Ahrens 41334. Marxzell, Brach Siegen east of Schielberg, 325-335 m, *Abies*; Ahrens s.n. Central Black Forest: Lahr, Sulz, Sulzbachtal, along forest trail left side of the valley, 240 m; 29.7.2009, Wirth & Ahrens 41280. Bleichheim near Herbolzheim, E Muckental, Bleiche Valley, 270 m; 29.7.2009, Wirth & Ahrens 41254; Schenkenzell, Nachtloch, 410 m; Wirth 41284. Southern Black Forest: Brenden, Schwarzatal below Eichholz, bottom of valley, 580 m; 17.8.2009, Wirth & Wirth 41285.

Fellhanera viridisorediata Aptroot, M. Brand & Spier (Plate 2A-D)
The thalli observed here are comparatively thin when compared to the type and those of other localities, and the apothecial margins are delicate. The species is to be considered substrate-indifferent, since it is usually reported from bark of branches and trunks, but here was found abundantly foliicolous on *Abies* with well-developed and numerous apothecia and relatively few soralia. *Fellhanera viridisorediata*, especially when the thallus is thin, closely resembles the neotropical *Fellhanera misionensis*. The two species agree in practically all morphological and anatomical features, except for the formation of soralia in *F. viridisorediata* and the production of roccellic acid.

Germany, Baden-Württemberg. Northern Black Forest: Marxzell, Brach Siegen east of Schielberg, 325-335 m, on *Abies;* 13.6.2009, Ahrens s.n.; ibid., 13.6.2009, on *Picea*, Ahrens s.n.; ibid. 29.6.2009, Ahrens & Wirth 41165. Central Black Forest: Ettenheim, Ettenheimmünster, valley of the Dörlinbacher Grundbächle, 275 m, on *Abies*; 29.7.2009, Wirth & Ahrens 41256, 41260. Lahr, Sulz, Sulzbachtal, along forest trail, 280 m; 29.7.2009, Wirth & Ahrens 41277. Schenkenzell, Heubachtal, bottom of valley south of Hirschengrund, 475 m; 16.8.2009, Wirth 41292; Schenkenzell, Nachtloch, 410 m; Wirth 41284. Southern Black Forest: Sulzburg, Fliederbachtal, bottom of valley, 380-400 m, on *Abies*; 9.9.2009, Wirth 41330.

Fellhaneropsis myrtillicola (Erichs.) Sérus. & Coppins (Plate 2E-F)
This substrate-indifferent lichen is one of the more common species on *Abies* needles in the Black Forest, especially under humid conditions. It is much rarer on *Picea* needles or *Rhododendron* leaves. It mostly forms thalli with pycnidia only, but in some collections (e.g. on *Rhododendron* leaves), the small, dark, emarginate apo-

thecia were also found. The species appears to be developing fast, with pycnidial thalli usually found on 2-year old branchlets. On 6- to 7-year old branchlets, it can dominate the community. Thalli with apothecia, found in two collections on *Abies* needles and *Rhododendron* leaves (Grobbachtal near Geroldsau, together with *Bacidina chloroticula* and *Fellhanera bouteillei*), resemble those of the neotropical *Fellhanera emarginata* Lücking and *F. obscurata* Lücking (Lücking 2008), and without the characteristic pycnidia are difficult to separate from the latter two if certain anatomical details such as excipulum structure and hypothecium color are not properly observed.

Germany, Baden-Württemberg. Northern Black Forest: Baden-Baden, Geroldsau, below Geroldsauer water fall, 280-300 m, on *Rhododendron*; 29.6.2009, Ahrens & Wirth 41333. Central Black Forest: Alpirsbach, Aischbachtal, 550 m; 16.8.2009, Wirth 41280. Ettenheim, Ettenheimmünster, valley of the Dörlinbacher Grundbächle, 275 m, on *Abies*; 29.7.2009, Wirth 41295. Lahr, Sulz, Sulzbachtal, along forest trail left side of valley, 210 m; 29.7.2009, Wirth & Ahrens 41334.; ibid., 340 m; 29.7.2009, Wirth & Ahrens 41307. Schenkenzell, Heubachtal, across Mantelhof, 390 m, on *Abies* at forest margin; 16.8.2009, Wirth 41290, 41296 (with *Jamesiella anastomosans*); ibid., bottom of valley south of Hirschengrund, 475 m; 16.8.2009, Wirth 41292. Schiltach, Heubachtal, ca. 400 m, 16.8.2009, Wirth 41335; ibid., south before Eulersbach, Höllgraben, fir forest, 480 m; 16.8.2009, Wirth 41283. Wolfach, Heubachtal, ca. 450 m; 16.8.2009, Wirth 41289. Southern Black Forest: Brenden, Schwarzatal below Eichholz, bottom of valley, 580 m; 17.8.2009, Wirth & Wirth 41285; ibid., Schwarzatal between Eichholz and Leinegg, bottom of valley, 550 m; 18.8.2009, Wirth & Wirth 41286. Sulzburg, Fliederbachtal, bottom of valley, 455 m, on *Abies*; 9.9.2009, Wirth 41331.

Gyalectidium setiferum Vězda & Sérus. (Plate 3A-E)
This is the only truly foliicolous species in the Black Forest. It is characterized by small, densely setose thalli which produce conidial diahyphae at the base of the setae. *Gyalectidium setiferum* is known from oceanic areas in western Europe (France, Great Britain, Spain) and the Colchis (Sérusiaux 1993). It is most often found on *Buxus sempervirens*, more rarely on *Abies* and *Laurocerasus*. In the Black Forest, *G. setiferum* is presently known from four localities. In the southern Black Forest locality, it was recorded from 15 *Abies* trees, often together with *Fellhanera bouteillei*, but rarely on the same needles. Sometimes up to 50 thalli were observed on individual needles and a single-year branchlet can support several hundred thalli. Interestingly, nearby *Buxus* shrubs did not support this species. In the central Black Forest, *G. setiferum* was found at two localities, with few thalli for example near Bleichheim on a single *Abies* tree together with *Fellhanera bouteillei, F. subtilis,* and *Fellhaneropsis myrtillicola*, and more abundantly near Schiltach on several fir trees together with *Fellhanera bouteillei, Fellhanera viridisorediata*, and *Fellhaneropsis myrtillicola*, in both cases together with the liverworts *Microlejeunea ulicina* and *Metzgeria temperata* (occurrence of foliicolous liverworts Ahrens in prep.). At the latter locality, it was well-developed on four- and five-year old needles with young thalli already colonizing two-year old needles. *Gyalectidium setiferum* is to be expected at other localities in the Black Forest and in the Vosges.

Germany, Baden-Württemberg. Central Black Forest: Bleichheim near Herbolzheim, E Muckental, Bleiche Valley, 270 m; 29.7.2009, Wirth & Ahrens 41253. Schiltach, before Eulersbach, Höllgraben, fir forest, 460 m, 16.8.2009, Wirth 41336; ibid., 480 m; 16.8.2009, Wirth 41283. Southern Black Forest: Sulzburg, Bad Sulzburg, below public bath, near bottom of valley, 440 m; 24.7.2009, Wirth 41243. Between Sulzburg and Bad Sulzburg, near bottom of valley, 440 m, on *Abies*; 24.7.2009, Wirth 41242, 41305. Bollschweil, Möhlintal, 410 m, along the Möhlin, on *Abies*, 9.9.2009, Wirth 41327.

Scoliciosporum curvatum Sérus. (Plate 3F)
This is an oceanic, substrate-indifferent species more common in western Europe, but can be found at scattered localities in central Europe. It was found on leaves of *Laurocerasus* near Sulzburg together with free living algae. The species is somewhat unusual in the genus in having relatively broad ascospores that are lunular in shape and 1-septate. Most other species of *Scoliciosporum* have narrow ascospores superficially similar to those of *Bacidina*, but the latter can be distinguished by the usually yellowish apothecia and paraplectenchymatous excipulum. Most *Scoliciosporum* species are

considered fast-growing, which is also true of *S. curvatum* (Sérusiaux 1993) and often resemble algal colonies due to the tiny, easily overlooked apothecia.
Germany, Baden-Württemberg. Southern Black Forest: Sulzburg, Bad Sulzburg, on *Laurocerasus officinalis*, 455 m; 24.7.2009, Wirth 41252.

Key to foliicolous species of the *Fellhaneropsis myrtillicola* association in central Europe

1a Identification by means of apothecia 2
1b Identification by means of conidiomata or other thallus characters 7

2a Ascospores long-tapering to needle-shaped, more than ten times as long as broad, spirally twisted in the asci; apothecia pale yellow, with paraplectenchymatous exciple; thallus grey-green, farinose to granulose . . . . . ***Bacidina chloroticula***
2b Ascospores ellipsoid to oblong or halfmoon-shaped, less than ten times as long as broad, irregularly arranged in the asci; apothecia and thallus variously colored and shaped . 3

3a Ascospores halfmoon-shaped; apothecia with hyphal excipulum, emarginate, brown; thallus grey-green, granular . . . . . ***Scoliciosporum curvatum***
3b Ascospores ellipsoid to oblong; apothecia with para- or prosoplectenchymatous excipulum, variously shaped and colored 4

4a Apothecia small, emarginate, dark brown, with prosoplectenchymatous excipulum; ascospores oblong, 3-septate; pycnidia common, producing filiform, curved conidia . . . . . ***Fellhaneropsis myrtillicola***
4b Apothecia conspicuous with thin but distinct pale margin and pale yellow to dark brown disc, with paraplectenchymatous excipulum; ascospores ellipsoid, 1-3-septate; pycnidia, if present, forming pear-shaped or oblong conidia 5

5a Apothecia with dark brown disc; thallus with diffuse, pale green soralia; ascospores 1-septate . . . . . ***Fellhanera viridisorediata***
5b Apothecia with pale yellow to orange disc; thallus lacking distinct soralia but sometimes dissolved into soredia-like granules; ascospores 1-3-septate 6

6a Ascospores 3-septate; thallus grey-green, composed of small, compact patches; pycnidia usually absent . . . ***Fellhanera subtilis***
6b Ascospores 1-septate; thallus usually bluish grey-green, farinose to granular; pycnidia common, producing pear-shaped conidia . . . . . ***Fellhanera bouteillei***

7a Thallus resembling icing or frosting (with cartilaginous cortex), with numerous translucent to white setae which at their base produce moniliform conidial diahyphae intermingled with algal cells . . . ***Gyalectidium setiferum***
7b Thallus lacking setae 8

8a Pycnidia absent; thallus diffusely sorediate, containing roccellic acid; soralia pale green . . . . . ***Fellhanera viridisorediata***
8b Pycnidia present; thallus not sorediate although sometimes dissolved into soredia-like granules; chemistry different or substances absent 9

9a Thallus farinose to granulose, bluish grey-green, with white pycnidia that produce pear-shaped conidia. . . . . ***Fellhanera bouteillei***
9b Thallus composed of small, compact patches, grey-green, with dark grey to blue black pycnidia that produce filiform, curved conidia . . . . . ***Fellhaneropsis myrtillicola***

Apart from the species discussed above, at the cited localities we also found a few accidentally foliicolous species growing on leaves or needles: *Physcia tenella, Hypogymnia tubulosa, Melanohalea exasperatula, Hypotrachyna revoluta, Parmelia sulcata, Physcia adscendens, Agonimia* spec., *Normandina pulchella*, *Candelariella reflexa*, *Bacidina* aff. *arnoldiana*, and *Jamesiella anastomosans* (Plate 4). The first three species were found at almost all localities that also harbored *Bacidina chloroticula* and *Fellhanera bouteillei.*
At one locality, we also found *Strigula*-like leaf deformations but could not find any fungal structures associated with them (Plate 4). The genus *Strigula* includes the only foliicolous species that penetrate the leaf cuticle, because the photobiont is an otherwise leaf-parasitic alga of the genus *Cephaleuros* (Lücking 2008). *Strigula* thalli therefore have a very characteristic appearance usually forming numerous bright green "bumps" on the colonized leaves, very different from other foliicolous lichens. The bright green

deformations found here very closely resemble such thalli but are apparently only formed by a free-living *Cephaleuros* species. Already Lettau (1940) discovered these structures in the *Buxus* forest near Grenzach and described them as „*... blaßgrünliche, schwach blasig aufgewölbte, um 0.2-0.5 mm große, rundliche, hier und da zusammenfließende Fleckchen. Die Untersuchung ergab eine Alge, die unter der Cuticula dieser Blätter wuchs. Es handelt sich um die gleiche Alge (Phycopeltis spec. cf. epiphyton Mill.), die die Gonidien der S. buxi bildet. …. Pilzhyphen und Fruktifikationen eines Pilzes konnte ich jedoch nicht finden. Also gewissermaßen eine nicht lichenisierte S. buxi!*" [*... pale green, slightly inflated, about 0.2-0.5 mm large, rounded, sometimes confluent patches. The study resulted in an alga which grew beneath the cuticle of those leaves. It is the same alga (...) that forms the gonidia of S. buxi. ... However, I could not find fungal hyphae and fructifications of a fungus. A non-lichenized S. buxi, so to speak!*"]. Lettau's description perfectly matches our own findings, although his interpretion of a non-lichenized *S. buxi* is incorrect, as it is a non-lichenized alga, not a non-lichenized fungus. It is possible that the non-lichenized alga found here and the photobiont of *S. buxi*, a species so far unknown from central Europe, belong to the same species and the structures found here could be considered "precursors" of a *Strigula* lichen (with fungal hyphae present but not discernable). In tropical *Strigula* species, it can often be observed that younger leaves have non-lichenized *Cephaleuros* thalli present and in older leaves these become "infected" with fungal elements to eventually form the *Strigula* lichens.

3 Discussion

All foliicolous lichens reported here were collected between 200 m and 550 m, with the exception of *Bacidina chloroticula*, *F. bouteillei* and *F. myrtillicola*. This corresponds to the lowland ("kollin") to submontane levels, which are characterized by relatively high annual mean temperatures. Most localities are situated in valleys in proximity to creeks and protected from wind, and all in valleys with creeks and rivers flowing westwards into the river Rhine, not eastwards into the Danubian river system with its rather cold valleys. Annual precipitation exceeds 1000 mm according to readings from nearby stations, resulting in a mild oceanic climate, which is more typical of coastal western Europe. Two interesting findings are *Gyalectidium setiferum* and *Scoliciosporum curvatum*, which hitherto were only known from localities with more or less oceanic climate in western Europe (Sérusiaux 1993).

The high abundance of several species on needles of *Abies* is of particular interest. At very humid sites, taxa such as *Fellhanera bouteillei*, *Bacidina chloroticula* and especially *Fellhaneropsis myrtillicola* appear constantly in the biota of *Abies* forests in proximity to creeks. We consider richly structured fir forests with mixed young and mature and old trees and with variable light conditions as optimal for the growth of *Bacidina chloroticula* and other foliicolous lichens. At more illuminated microsites, along creeks, trails, and slopes, *Fellhanera* species become common, as well as *Gyalectidium setiferum*, although the latter also requires a high level of humidity, such as frequent fogs and high precipitation (> 1000 mm). There is an intrinsic similarity of these communities to those described by Killmann et al. (2004) on *Buxus* in valleys of the Mosel. The communities found in the Black Forest are, however, richer in species and also include with *G. setiferum* a obligately foliicolous species, and they are dispersed over many different localities. In general, it appears that there is a characteristic foliicolous lichen association (Fellhaneretum myrtillicolae Spier & Aptroot) all across central Europe consisting of *Bacidina chloroticula*, *Fellhanera bouteillei*, *F. subtilis*, *F. viridisorediata*, *Fellhaneropsis myrtillicola*, and *Gyalectidium setiferum* (Poelt & Vězda 1992, van den Boom & Sérusiaux 1996, Hafellner & Türk 2001, Killmann et al. 2004, Cézanne et al. 2008). Judging from the habitat conditions in the Black Forest, there is little doubt that similar lichen associations also occur in the Vosges (eastern France).

Though foliicolous lichen communities have not previously been reported from the Black Forest, their occurrence is not really surprising, since a humid and mild, albeit not particularly warm-humid, climate is locally developed. Especially the area around Baden-Baden is known for its mild climate, which corresponds with the fact that the only known locality of the pantropical epiphyte *Heterodermia leucomela* was found here. On the other hand, apart from the foliicolous communities, no other rare or remarkable species were found at most of these sites so far, except for *Gyalidea hyalinescens*, which Arnold collected more that 100 years ago at the Geroldsauer water fall (Bausch 1869), and *Hypotrachyna*

revoluta (Wirth 1995). At the localities of *Gyalectidium setiferum* only, also some rare, oceanic epiphytes, including *Usnea ceratina, Fuscidea lightfootii, Parmotrema arnoldii, Nephroma parile*, and *Peltigera collina* are found. *Hypotrachyna revoluta* was found at most localities; its thalli usually overgrow the needles starting from the branchlets.

An interesting question is whether these foliicolous communities are relicts or appeared more recently due to a combination of global warming and improved air quality. Air quality improved in central Europe since the mid 80s, as shown for example by lichen mapping studies (Kirschbaum & Hanewald 1998, Wirth 1993), and the 13 warmest years since the beginning of systematic temperature records all occurred after 1990 (Zorita et al. 2008). It has even been suggested that improved air quality accelerates global warming (Andreae et al. 2005). The foliicolous lichens found here spread rather easily by vegetative propagules (soredia, thallus granules, conidia, diahyphae) which are adapted to dispersal by both wind and rain. For example, *Scoliciosporum curvatum* is considered an easily spreading species (Sérusiaux 1993) and occurrences in parks and gardens in Scotland and Northern Ireland demonstrate that this species quickly colonizes newly available substrata. Since the Black Forest is one of the best known areas in Germany in terms of its lichen biota and has been thoroughly studied by V. W., and foliicolous lichens have been searched for in this area by R. L., relatively recent establishment of these communities seems more likely. Otherwise, more historic records of these lichens such as those by Lettau (1940) should be available and it would also be hard to explain that foliicolous communities have been overlooked at so many localities. Other reports of foliicolous lichen communities in central Europe are also quite recent (Poelt & Vězda 1992, van den Boom & Sérusiaux 1996, Hafellner & Türk 2001, Killmann et al. 2004, Cézanne et al. 2008).

Since the occurrence of foliicolous lichen communities in central Europe appears to be highly correlated with warm-humid climatic conditions (Sérusiaux 1993, Llop & Gómez-Bolea 2006), any change in such conditions would result in visible changes of the lichen communities, such as spreading or disappearance from known sites, as well as species composition. Thus, independent of these communities being an overlooked relict or the result of recent establishment, their study opens possibilities to their use as passive monitors of changes in climate and air quality. On the other hand, while increasingly warm-humid climate might promote the spreading of foliicolous lichen communities in parts of central Europe, these organisms appear to be very susceptible to forest management and habitat changes, a factor that has to be taken into consideration. It is therefore necessary to closely monitor these communities and conduct a more extensive inventory to determine their baseline distributions and abundances before using them as bioindicators of any sort. *Gyalectidium setiferum*, for example, could be a suitable indicator species of environmental health, as it responds to changes in humidity and habitat structure and is easily recognized in the field. Using lichens as bioindicators is of course not new and especially not in Germany, where environmental monitoring with lichens has been standardized (Bartholmess et al. 2004). However, the advantage of foliicolous lichens is their comparatively fast development: whereas corticolous and saxicolous species take many years or decades to develop substantial communities, foliicolous lichens such as *Gyalectidium* reach maturity after as little as one year (Sérusiaux 1989, Lücking 2008). Together with continuous leaf renewal, this provides a much more dynamic system than lichens on bark and rock surfaces.

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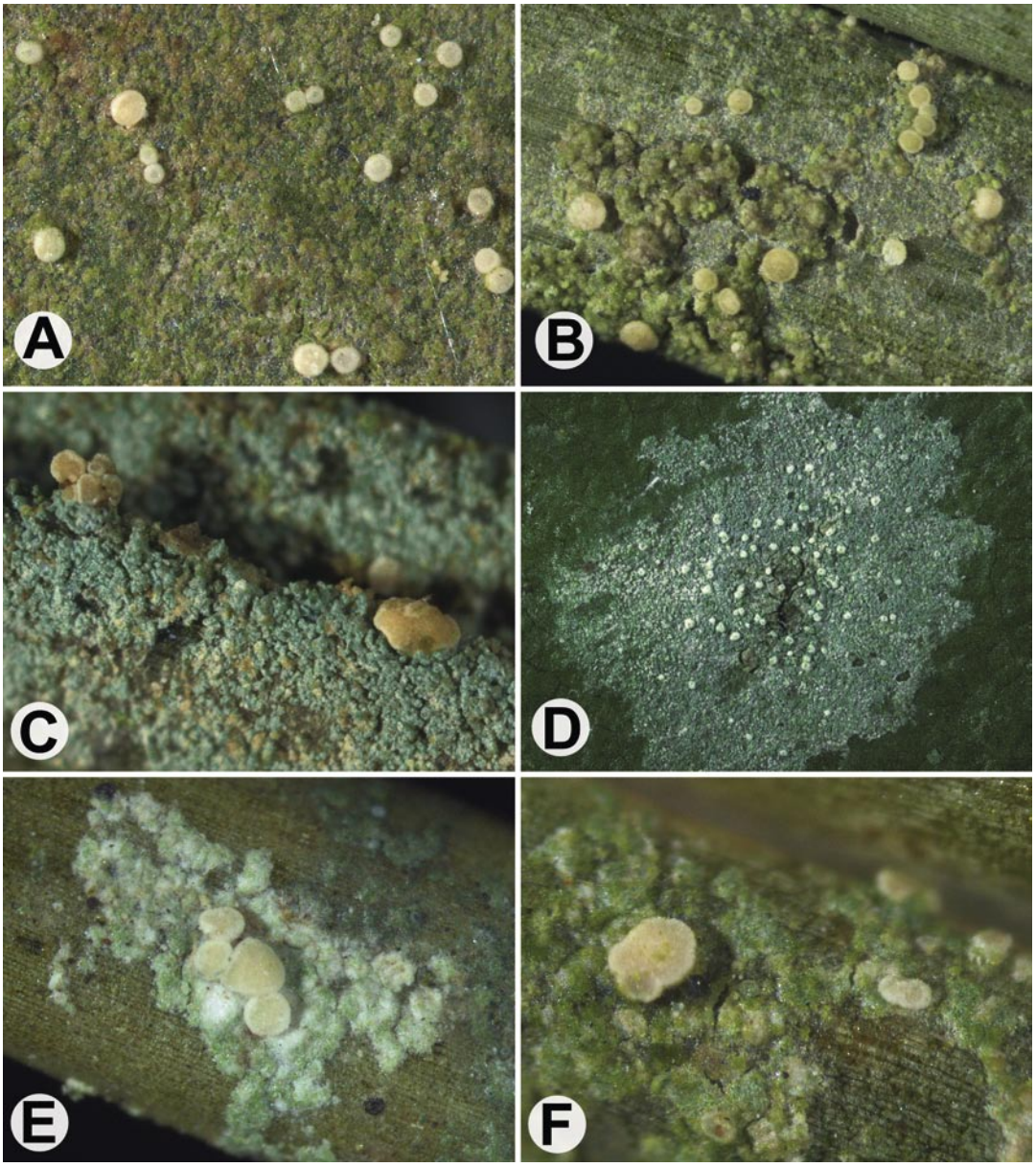

Plate 1: Foliicolous lichens. A-B, *Bacidina chloroticula*, thalli with apothecia (largest apothecia about 0.3 mm diam.) C-D, *Fellhanera bouteillei*, thalli with apothecia (C) and pycnidia (D; large apothecium in C 0.4 mm diam.; pycnidia in D 0.1 mm diam. E-F, *Fellhanera subtilis*, thalli with apothecia (largest apothecia about 0.3 mm diam.). All photographs by R. L.

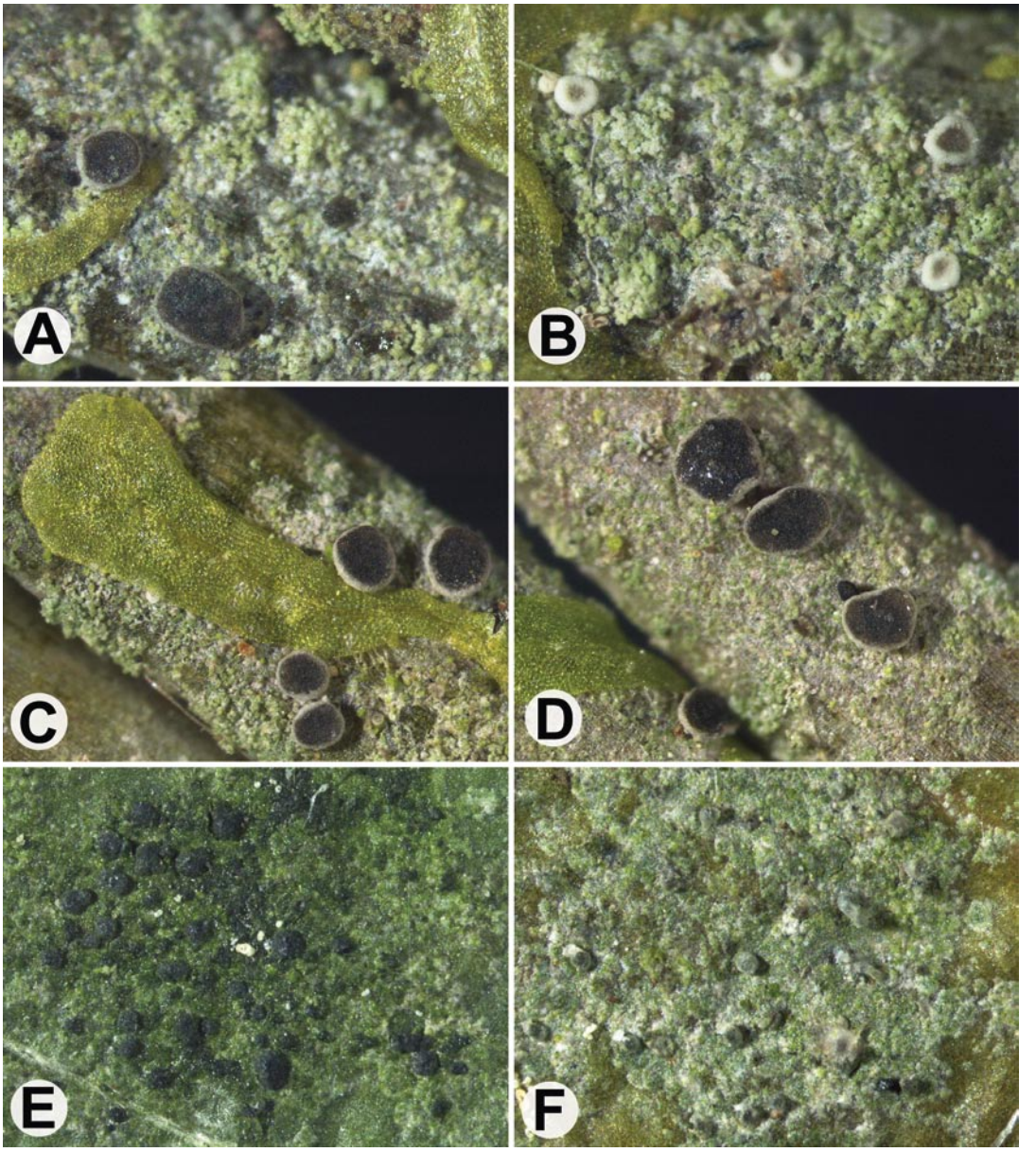

Plate 2: Foliicolous lichens. A-D, *Fellhanera viridisorediata*, thalli with apothecia and soralia (A showing soralia, B showing young apothecia; largest apothecia in A, C and D 0.4 mm diam., apothecia in B 0.2 mm diam.). E-F, *Fellhaneropsis myrtillicola*, thalli with apothecia (E) and pycnidia (F; apothecia 0.2 mm diam.; pycnidia 0.1 mm diam.). All photographs by R. L.

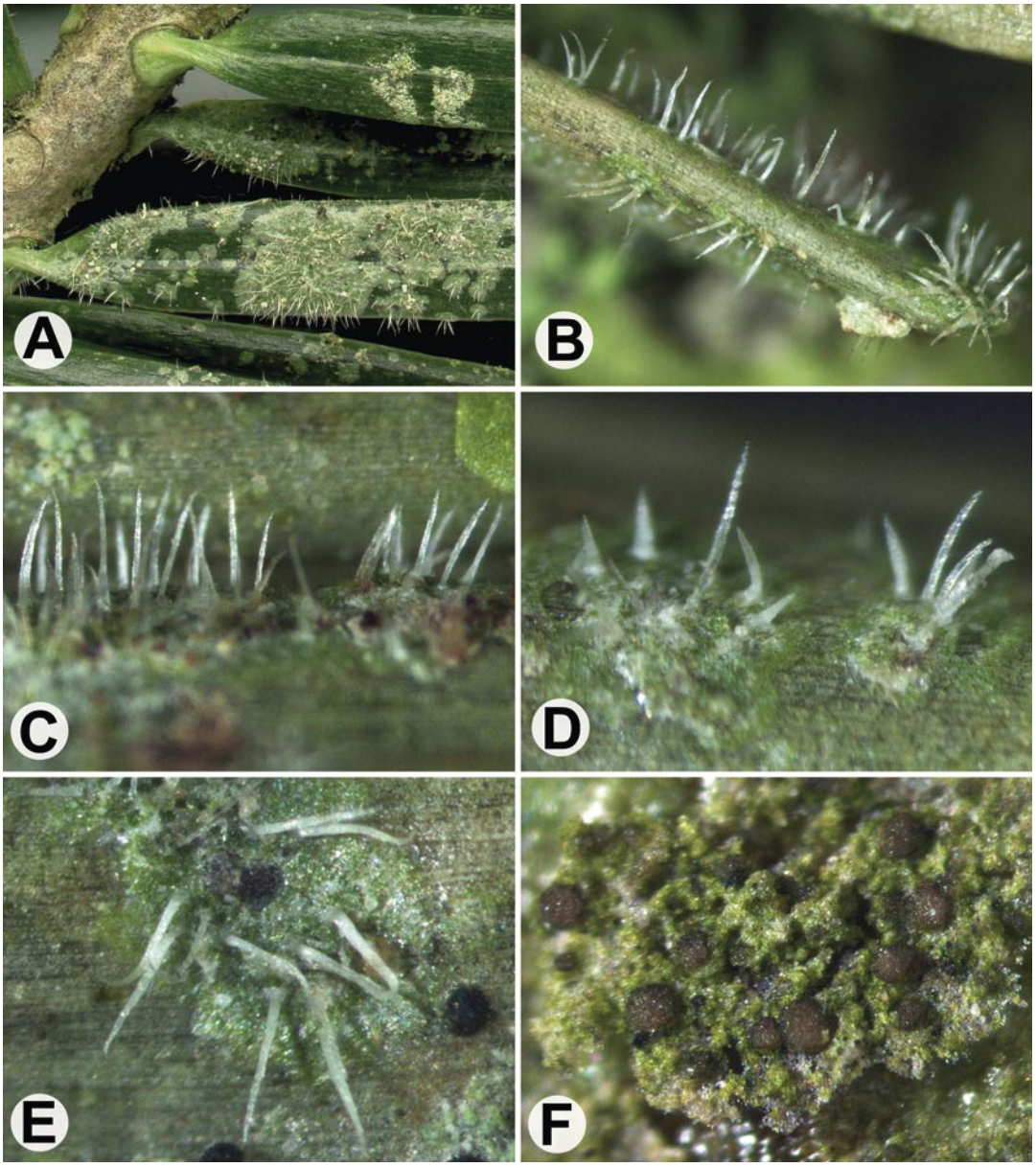

Plate 3: Foliicolous lichens. A-E, *Gyalectidium setiferum*, thalli with setae (hyphophores; setae about 0.3 mm high and needles in A about 2 mm wide). F, *Scoliciosporum curvatum*, thallus with apothecia (apothecia about 0.2 mm diam.). All photographs by R. L. except A (ALEXANDER RIEDEL, Karlsruhe).

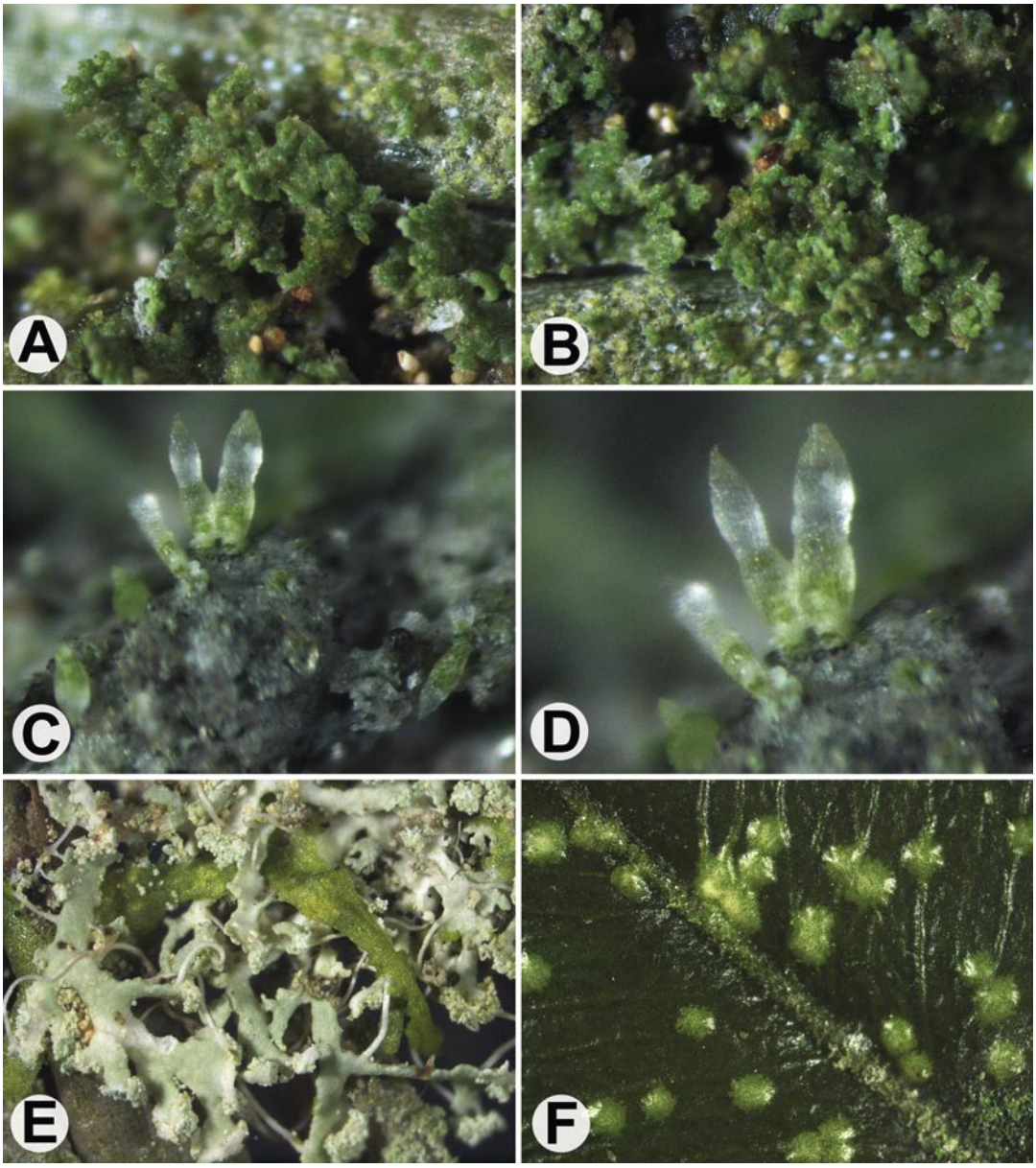

Plate 4: Accidentally foliicolous lichens (selected). A-B, *Agonimia* spec., squamulose thalli (thalli about 1 mm wide). C-D, *Jamesiella anastomosans*, thlasidia (isidioid hyphophores; largest hyphophore about 1 mm high and 0.2 mm wide). E, *Physcia tenella*, foliose thallus (lobes around 1 mm wide). F, *Strigula*-like leaf deformations on *Buxus* (largest patches around 0.5 mm diam.). All photographs by R. L.