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Stictis s. lat. (Ostropales, Ascomycota) in northern Scandinavia, with a key and notes on morphological variation in relation to lifestyle

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ABSTRACT

The closely related genera *Carestiella*, *Schizoxylon* and *Stictis* (Stictidaceae, Ostropales, Ascomycota) are revised in northern Scandinavia, and a revised phylogenetic hypothesis, including all seven species of this group in the area, is presented. A key to the species of *Stictis* s. lat. (including *Carestiella*, *Schizoxylon* and *Stictis*) in Northern Scandinavia is presented. *S. albescens* and *S. confusum* are described as new to science, and the new name *S. brunnescens* is introduced for *S. mollis* ssp. *populorum*, when treated as a distinct species. *C. socia* and *S. albescens* are the only representatives of their genera in northern Scandinavia, but a total of five species of *Stictis* are present in the area (*S. brunnescens*, *S. confusum*, *S. mollis*, *S. populorum* and *S. radiata*). Substantial within-species variation in ascoma morphology and wall pigmentation is revealed and discussed, and found to correlate with fungal lifestyles; optional lichenization apparently affects several details in fungal anatomy and morphology.

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Introduction

The genus *Stictis* and the closely related *Carestiella* and *Schizoxylon* (Stictidaceae, Ostropales, Lecanoromycetes) constitute a large group of predominantly saprotrophic discomycetes. The taxonomy and nomenclature of Stictidaceae was thoroughly revised on a worldwide scale by Sherwood (1977a,b), including wholly revised generic delimitations. *Stictis* itself had already been suggested to be congeneric with, and an older synonym to, the lichen *Conotrema* (Gilenstam 1969), as the similarities in the characteristics of the ascoma, ascus and ascospore were substantial. Sherwood (1977a), however, refrained from merging the two genera, as a future splitting of the still presumably

heterogeneous *Stictis* was likely to result in the revival of *Conotrema*. Recent phylogenetic analyses of DNA sequence data (Wedin et al. 2004, 2005), on the contrary, suggest that lichenized and saprotrophic species within the *Stictis*–*Conotrema* complex do not form distinct monophyletic groups corresponding to either the genera or the species as understood at that time.

Wedin et al. (2004) studied the relationships between lichenized and saprotrophic taxa within northern Scandinavian *Stictis*–*Conotrema* representatives in detail, using phylogenetic species recognition based on congruence of multiple gene genealogies. Three phylogenetic species were identified, all containing both lichenized and saprotrophic specimens. These were the first known cases where individuals of the same

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fungal species have the option to develop either as lichens or as saprotrophs depending on the substrate (bark or wood of *Populus*), and in this way increase their ecological amplitude. Wedin et al. (2004) coined the term 'optional lichenization' for this phenomenon and predicted this to be a strategy in fungi adapted to successional habitats that are unpredictable in time and space, as the *Populus*-stands in the boreal coniferous forests. Here, we will give detailed descriptions of the species showing optional lichenization. Although the different morphs of these species differ considerably in habit and morphology, most anatomical characteristics do not vary according to lifestyle.

Stictis is characterized (Sherwood 1977a) by having a more or less orbicular ascoma that opens by a pore, a margin lined by periphysoids that extend the whole length of the margin, a hymenium that splits away from the margin when dry, and filiform, thin-walled, multiseptate ascospores that do not disarticulate into part-spores. We use a wider generic concept regarding *Stictis*, following the suggestions given by Wedin et al. (2004, 2005), and include species that also live as lichens, and thus would fit the genus *Conotrema*. From our phylogenetic analyses, we can so far conclude that even if *Stictis* eventually would better be treated as several genera, it is unlikely that the name *Conotrema* would ever be available for one present in our area. The type species of these two generic names (*S. radiata*, *C. urceolatum*) together form a group indicating that they are more closely related to each other than to other sampled species of these two genera. Gilenstam (in Wedin et al. 2005) combined both *C. urceolatum* and *C. populorum* into *Stictis*. However, we find it useful to retain the anatomically very distinct genera *Schizoxylon* and *Carestiella* following Sherwood (1977a,b), even if this is based on morphological grounds only, and results in *Stictis* in our circumscription becoming a paraphyletic group. This, still unnatural, generic concept should be seen as a preliminary step until further studies including material from other parts of the world give us a better understanding of the groups within this large genus. Both *Stictis* and *Schizoxylon* are large and potentially heterogeneous genera, and our limited sample of species is naturally much too small to base a revised classification on. In the present paper, we will refer to the genera *Stictis*, *Schizoxylon* and *Carestiella* as 'Stictis s. lat.' when needed, indicating that they are very closely related, and that the generic delimitation is unclear.

Currently (Eriksson OE, Fungi of Sweden: Ascomycota. <http://www.umu.se/myconet/ascoc/indexASCO.html>), five representatives of *Stictis* are known from Sweden; *S. cladoniae*, which is not an ostropalean fungus (Sherwood 1977a: 166), *S. mollis* subsp. *mollis*, *S. mollis* subsp. *populorum*, *S. populorum* (as *C. populorum*), and the type species *S. radiata*. Eriksson also reports one species of *Schizoxylon* which we, however, have not found in our area: *S. berkeleyanum*. During our fieldwork in northern Scandinavia, a number of ostropalean taxa new for the area were discovered, including undescribed representatives of *Stictis* and *Schizoxylon*. These were already included in our earlier phylogenetic analyses (Wedin et al. 2004, 2005). It is clear that the ostropalean fungi are very poorly known in northern Scandinavia, largely due to their small size and inconspicuous habit. Investigations of these fungi, especially those growing on *P. tremula* (aspen) and *Salix caprea* (goat willow), were undertaken during 2000–2004 in order to learn more about the group in the region. This paper summarizes

our taxonomic results from this period, including an updated phylogenetic hypothesis of all known species of *Stictis*, *Schizoxylon* and *Carestiella* in the area, the description of new species, and to report on some of the detailed anatomical work undertaken. In particular, we wish to present a key and detailed descriptions of the representatives of *Stictis* s. lat. in northern Scandinavia. We also would like to discuss the variation in habit, morphology and anatomy, apparently caused by the different lifestyles in the species that show optional lichenization.

Material and methods

This investigation is mainly based on our own collections, which will be deposited in UPS. We have conducted fieldwork in the provinces of Hälsingland, Jämtland, Ångermanland, Västerbotten, Norrbotten, Lycksele Lappmark and Lule Lappmark in northern Sweden, and in Troms fylke in Norway. In addition, we received material on loan from DAOM, GZU, H, S, UME and UPS. All types cited have been investigated, unless otherwise stated.

Hand-cut sections of the ascomata were made for preliminary identification and spore measurements; freezing microtome sections, usually 20–30 µm thick, were produced for anatomical investigations. Measurements given in the text are standardized as follows: diameters and widths are measured at the widest point; only asci containing mature spores were measured; and the width of the ascus was taken at the base of the apical thickening; the length and the width of the spores were usually measured when still in the ascus, as justified by Sherwood (1977a). However, it is very difficult to make accurate spore measurements in many of these species. In all species investigated here, with the exception of *Carestiella socia*, the spores are nearly as long as the asci. All measurements and photographs were taken in lactic blue (cotton blue in lactic acid, glycerol, water 1:2:1), unless stated otherwise. Lugol's iodine solution was used for iodine tests, both with and without pre-treatment with potassium hydroxide. It should be noted that the positive amyloid reactions, which are present in the hymenium of all species treated here, may need several flushes of Lugol's solution to develop, and are often comparatively pale and irregular.

Parsimony analyses including all seven species of *Stictis* s. lat. known from northern Scandinavia were performed using an updated data matrix from Wedin et al. (2005), combining data from two molecular markers (a continuous stretch of the nuclear ITS and LSU rDNA, and mtSSU rDNA). The DNA-sequences used and methods were taken from either Wedin et al. (2004), Wedin et al. (2005), or produced here (Table 1). Three representatives of *Lecanorales* were chosen as outgroup. In the species where optional lichenization is known to occur (Wedin et al. 2004), we included at least one lichenized and one saprotrophic sample, and for the two species newly described here, we also included sequences from the holotype specimens. The combined data matrix was analysed with MP using PAUP 4.0b10 (Swofford 2002). Parsimony settings: steepest descent off, collapse branches if minimum length is 0, gaps are treated as missing data. Heuristic search settings: 1000 random addition sequence replicates with start from random

Table 1 – Sequences used in the phylogenetic analysis

Species	Specimen	mtSSU rDNA	Nuclear ITS and LSU rDNA
<i>Carestiella socia</i>	Sweden, Gilenstam 2410	AY661677	AY661687
<i>Carestiella socia</i>	Sweden, Gilenstam 2437a	AY661678	AY661682
<i>Schizoxylon albescens</i> , saprobe	Sweden, Gilenstam 2365	AY661680	AY661689
<i>S. albescens</i>, lichen, holotype	Sweden, Gilenstam 2696a	DQ401142	DQ401144
<i>Stictis brunnescens</i>	Sweden, Gilenstam 2359	AY661679	AY661688
<i>S. confusum</i>, lichen, holotype	Sweden, Wedin 7070	DQ401141	DQ401143
<i>S. confusum</i> , lichen	Sweden, Nordin 3222	AY527365	AY527336
<i>S. confusum</i> , saprobe	Sweden, Gilenstam 2609a	AY527353	AY523324
<i>S. populorum</i> , lichen	Sweden, Gilenstam 2618	AY527360	AY527331
<i>S. populorum</i> , lichen	Sweden, Gilenstam 2610a	AY527356	AY527327
<i>S. populorum</i> , saprobe	Sweden, Gilenstam 2440b	AY527350	AY527321
<i>S. mollis</i> , lichen	Sweden, Wedin 7200	AY527342	AY527313
<i>S. mollis</i> , saprobe	Sweden, Gilenstam 2445a	AY527347	AY527318
<i>S. urceolatum</i> , lichen	USA, Tibell 21500	AY661676	AY661686
<i>Cryptodiscus foveolaris</i>	Sweden, Gilenstam 2603a	AY661673	AY661683
<i>Odontotrema</i> sp. 1	Sweden, Gilenstam 2560	AY661674	AY661684
<i>Odontotrema</i> sp. 2	Sweden, Gilenstam 2601b	AY661675	AY661685
<i>Stictis radiata</i>	Sweden, Gilenstam 2449a	AY340532	AY527308
<i>S. radiata</i>	Sweden, Wedin 6493	AY527338	AY527309
<i>Thelotrema lepadinum</i>		AY340533	AY340576
Outgroup			
<i>Lecidea fuscoatra</i>		AY756401	AY756339
<i>Hypogymnia physodes</i>		AY756400	AY756338
<i>Physcia aipolia</i>		AY143406	AY300857

Newly produced sequences in bold face. All specimens housed in UPS.

trees, tree bisection–reconnection (TBR) branch swap, multiple trees saved. Uninformative characters and ambiguously aligned regions (defined by means of subjective inspection by eye) were excluded from the analyses. The polarity of the characters was assessed with outgroup comparison using three representatives of the *Lecanorales* as outgroup. Parsimony jackknifing for rapid identification of well-supported monophyletic groups (Farris et al. 1997) was performed in PAUP. Jackknife settings: 1000 jackknife replicates with ‘JAC’-emulation, nominal deletion of characters 37 %, full heuristic search, retain groups with frequency > 50 %. Heuristic search settings: ten random addition replicates with start from random trees, TBR branch swap, and multiple trees saved.

Results and discussion

Remarks on apothecial anatomy and terminology

A main feature in the description of genera and species in the *Stictidaceae* is the structure of the ascoma margin. The differentiation of various wall layers; their pigmentation and the formation of crystals have often been used as diagnostic characters. Sherwood (1977a) distinguished up to five layers in the ascoma wall of non-lichenized ostropalean fungi. She also compared her interpretation of ascoma wall structures with those described by Gilenstam (1969) in lichenized *Stictis* (*Conotrema*) species. We found it difficult, however, to use her terminology, and we will make some general comments below. The ascoma wall in the *Stictidaceae* is composed of layers

with different origin. In addition to the true exciple formed from the ascoma primordium (‘proper ascoma wall’ in our sense), there are also various amounts of host tissue remnants involved in forming the margin (compare for example Fig 9A with E). There is no clear delimitation between the proper ascoma wall and the surrounding hyphae in the *Stictis* species treated here; there is no well-delimited layer of densely packed hyphae, corresponding to Sherwood’s ‘stroma’ (as illustrated in Sherwood 1977a, fig. 3) in our taxa. This ‘stroma’ would clearly separate the true ascoma wall from surrounding vegetative parts of the margins. Sherwood (1977a: 15) defined vegetative parts of the ascoma wall composed by ‘disintegrating host tissue invaded by vegetative hyphae’ as a ‘thalline margin’. She claims (1977a, table 5) that the scleroplectenchymatous (second) layer described by Gilenstam (1969) in *Conotrema* would be corresponding to a ‘stromatic’ layer. However, in all Scandinavian *Stictis* species investigated by us, including the lichenized forms, the scleroplectenchymatous layer does contain considerable amounts of host tissue remnants and is thus, in our interpretation, homologous to Sherwood’s ‘thalline margin’ in the non-lichenized *Stictis* species. As there is no ‘stromatic’ layer, there is also no sharp border between this ‘thalline margin’ and the proper wall in mature ascomata. We have not studied the ontogenetic origin, but agree with Sherwood that this layer is most likely formed by vegetative hyphae. To avoid further confusion, we refer to this part of the wall simply as a layer including remnants of host tissue. In several species, as *St. populorum*, the ascoma wall hyphae are pigmented brown, and both the proper wall layer and the layer including remnants of host tissue adjacent

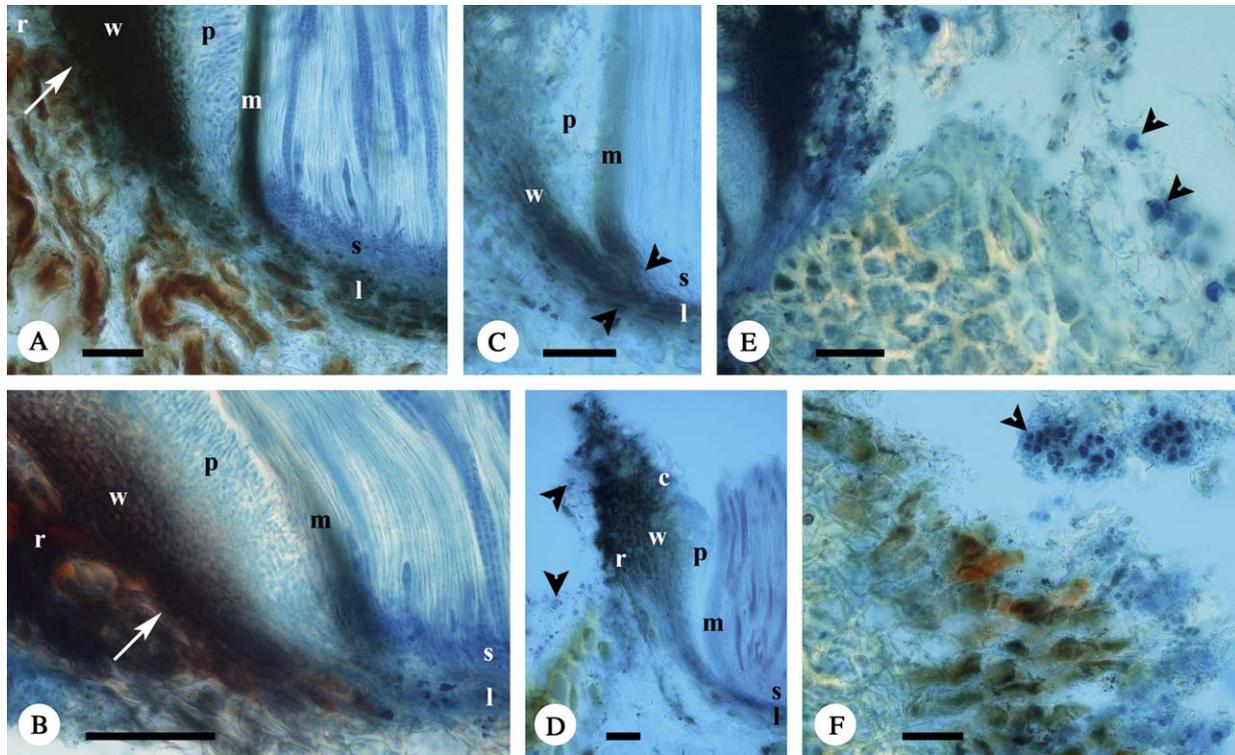


Fig 1 – Ascoma anatomy and lichenization. (A–B) Ascoma sections of *Stictis confusum*: (A) saprotrophic specimen with strongly pigmented marginal paraphyses and hypothecium/lower ascoma wall, but without carbonization of host tissue, Gilenstam 2609a; (B) lichenized specimen with carbonization of host tissue next to the proper ascoma wall, but only with faint pigmentation of hypothecium/lower ascoma wall and marginal paraphyses, Wedin 7051. (C–D) Ascoma sections of *S. mollis* (C) saprotrophic specimen with pigmented hypothecium/lower ascoma wall, without carbonization of host tissue, note lower ascoma wall hyphae in connection with the marginal paraphyses and the proper ascoma wall (arrowheads), Wedin 7209; (D) lichenized specimen with faint pigmentation of the proper ascoma wall and marginal paraphyses, and slight carbonization of host tissue; note scattered algae present in a thin ‘thalline margin’ (arrowheads), Wedin 7609. (E–F) Lichenization in *S. populorum* (E) scattered algae (arrowheads) on substrate surface in the vicinity of an ascoma, Nordin 2659, (F) algae (arrowhead) at the surface of whitish thallus patches (somewhat detached through sectioning), Wedin 7301. c, Crystalliferous layer; l, hypothecium/lower ascoma wall; m, marginal paraphyses; p, periphysoids; r, remnants of host tissue; s, subhymenium; w, proper ascoma wall; arrow indicates boundary between proper ascoma wall and host tissue. Bars = 30 µm.

to it can be so strongly pigmented that they together superficially appear as one single, blackish (‘carbonized’) wall layer (Figs 7B, E, 8A, C, 9A, E). The distinction between these layers is only possible when observing the presence of host tissue cells (Fig 1B). Whereas sometimes the entire host tissue surrounding the ascoma is ‘carbonized’ (Figs 7E, 9A), often only the remnants of host tissue close to the proper wall are ‘carbonized’ (Figs 7B, 8A, C, 9E). The ‘thalline margin’ mentioned by Gilenstam (1969) in *Conotrema* has no homologous structure in the non-lichenized morphs and thus does not correspond to any structure described by Sherwood. Gilenstam referred to a thalline margin in a lichenological sense, i.e. including algae. Such a ‘thalline margin’ can be inconspicuous and only form a thin layer above the layer including remnants of host tissue (Fig 1D), and it can be completely lacking in many mature ascomata, as illustrated by Gilenstam (1969, fig. 1).

In some ostropalean fungi the paraphyses at the margin of the hymenium are distinct from the majority of the paraphyses. Sherwood (1977a) uses the term ‘marginal paraphyses’ for an outermost ring of the hymenium formed by agglutinated

and differentially pigmented paraphyses. In addition, we have noticed in the investigated *Stictis* species, that these differentiated marginal paraphyses are a direct continuation of the hyphae of the hypothecium, and are thus surrounding the subhymenium (the layer of ascogenous hyphae) like a ring (Figs 1A–D, 6C, 9G). In some *Stictis* species (*S. confusum*, *S. mollis*, *S. populorum*) these marginal paraphyses are distinct. In *S. brunnescens*, only a faint pigmentation distinguishes these outermost hyphae.

Morphological and anatomical variation in species showing optional lichenization

In the lichenized morphs, the highly hydrophobic thallus does not form a distinct algal layer; the colour of the pale greyish area defining the extent of the colony on bark (Fig 2D), could mainly be due to dead, air-filled bark-cells. Scattered groups of lichenized coccoid algal cells can, however, be observed in these areas (Fig 1F) and in the vicinity of the ascomata (Fig 1D–E), but the degree of lichenization is probably variable.

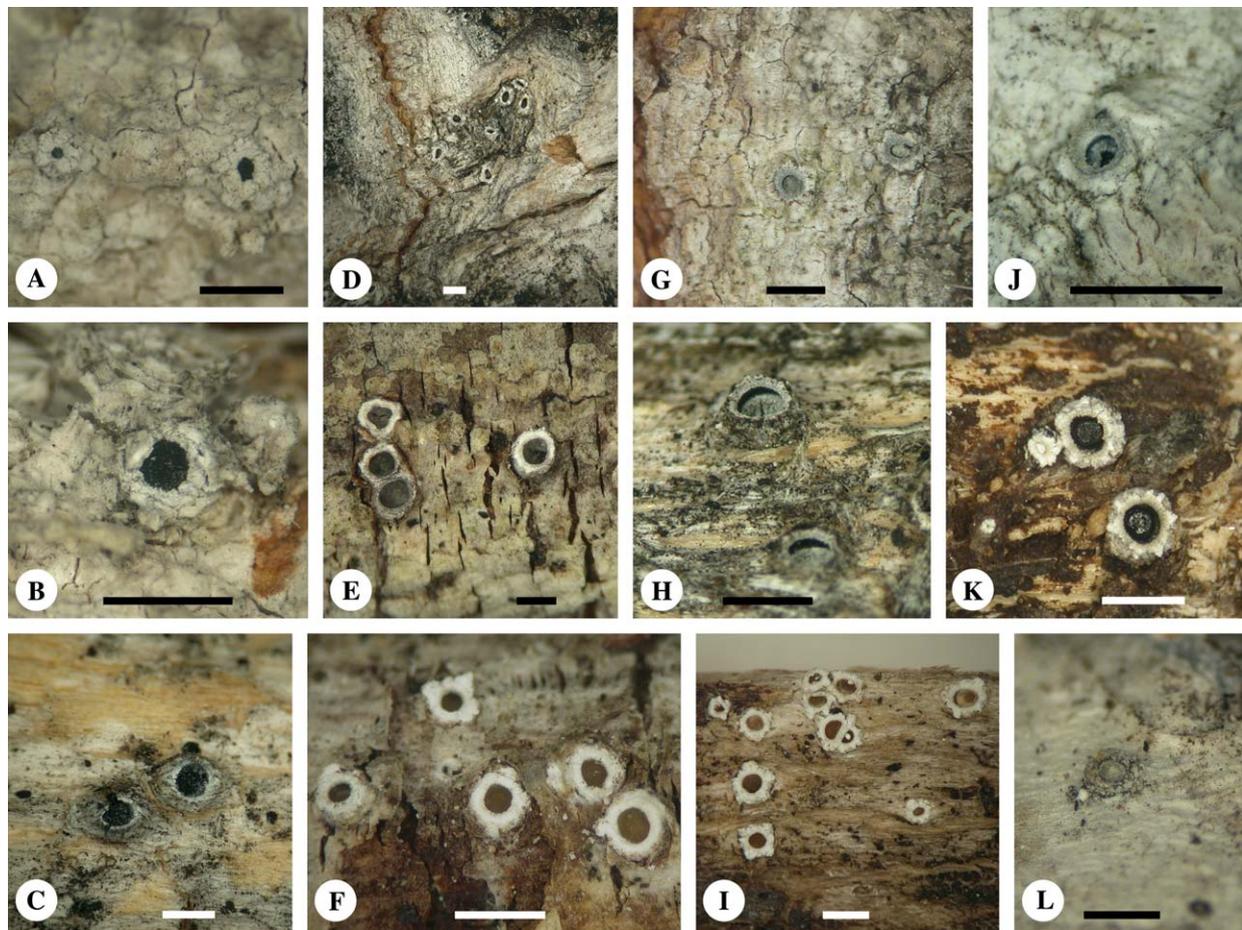


Fig 2 – Habit. (A–C) *Schizoxylon albescens* (A) young fruit bodies and (B) a mature fruit body, lichenized morph, Wedin 7345; (C) saprotrophic morph, Gilenstam 2443a. (D–E) *Stictis confusum* (D) lichenized morph, Nordin 3233, (E) saprotrophic morph, ascoma breaking through bark remnants, Gilenstam 2609a. (F) *S. brunnescens* ascoma on wood of a twig still covered by remnants of bark, Gilenstam 2614. (G–H) *S. populorum* (G) lichenized morph, Wedin 7301, (H) saprotrophic morph, Gilenstam 2661. (I) *S. radiata*, Wedin 7103. (J–K) *S. mollis* (J) lichenized morph, Wedin 7200, (K) saprotrophic morph, Wedin 7039. (L) *Carestiella socia*, Gilenstam 2660a. Bars = 1 mm.

The variation in morphology and habit in the species that occur both as lichens and as saprotrophs (*Schizoxylon albescens*, *Stictis confusum*, *S. mollis*, *S. populorum*) intrigued us for a long time. Superficially, the lichenized forms look distinctly different from their conspecific saprotrophic counterparts (Fig 2). The lichenized morphs have whitish thallus patches around their fruit bodies, which are often somewhat immersed (at least in younger stages) in the thallus and the bark of the host trunk. The fruit bodies of the saprotrophic morphs, however, are more often sessile on the decorticated wood substrate. The saprotrophic morphs also usually produce larger fruit bodies than the respective lichen. This provides more space for the periphysoid layer in the saprotrophs, which in general produce considerably better-developed periphysoids compared with the lichenized morphs.

In addition, the saprotrophs generally have a more heavily pigmented ascoma wall than the respective lichenized morphs (compare for example Fig 5A with C or 7B with E). The ascomata of the saprotrophs are usually more exposed on the substrate compared with the lichens, where the fruit bodies are usually

more immersed and often at least partly covered by host bark tissue. The pigmentation of the ascoma wall is also comparatively variable within the saprotrophic morphs. This, we have also attributed to differences in light exposure as ascomata originating beneath a cover of dead bark are considerably less pigmented compared with ascomata originating on highly exposed, bark-less wood. Variation in the amount of pigmentation could also be seen in sections of a single fruit body in a saprotrophic specimen of *S. mollis*, where the more exposed side was more pigmented than the other, which was covered by a considerable amount of bark tissue. The most variable part of the margin involves the remnants of host tissue around the ascoma. Here carbonization may sometimes be lacking (Fig 7A), or it can be prominent and even protrude into the host tissue below the ascomata (Figs 7B, 8E).

In the lower part of the ascoma wall, forming the underside of the ascomata, substantial variation between lichenized and saprotrophic specimens is found. In some lichenized specimens where the ascomata are deeply embedded in host tissue, the lower wall is very thin, often compressed or even

ruptured, and almost completely unpigmented (Figs 1B, 8C, 9B). This led Gilenstam (1969) to erroneously conclude that 'Conotrema' populorum lacked a lower ascoma wall. The saprotrophic morphs usually have a well-developed and distinct lower wall structure (Figs 1A, 8A, 9E). The lower wall is, however, composed of two layers. The lowermost layer is a continuation of the marginal proper ascoma wall. The innermost, which we refer to as 'hypothecium', as it is located between the subhymenium and the proper wall, is the layer to which the marginal paraphyses are connected (Figs 1A–C, 9B, F). The two lower wall layers are particularly distinct where the hypothecium is unpigmented and the continuation of the marginal proper ascoma wall is dark brown. In strongly pigmented saprotrophic morphs, it may not be possible to distinguish both these lower wall layers, apart from that their connection with either the marginal paraphyses, or the proper marginal ascoma wall, can be seen at the side of the ascomata.

Phylogenetic analysis

The analysed matrix consisted of a total of 573 unambiguously aligned parsimony-informative characters, of which 344 were from the nuclear rDNA partition and 229 from the mtSSU rDNA partition. Our parsimony analysis resulted in one most parsimonious trees of 1397 steps, CI = 0.6, RI = 0.7. This tree, with branch-lengths proportional to nucleotide changes and including jackknife support values for the nodes, is presented in Fig 3. Both *Carestiella* and *Schizoxylon albescens* are nested within *Stictis*, as currently delimited. *Stictis confusum* and *S. populorum* are sister species, as indicated by Wedin et al. (2004) and expected from their anatomical similarity. They are 'cryptic' species in the sense that they are extremely difficult to distinguish on morphology alone but easy to identify by molecular characteristics.

Key to the species of *Stictis* s. lat. in northern Scandinavia

- | | | |
|------|---|------------------------------|
| 1 | Disc ochraceous, glossy, never pruinose..... | 2 |
| | Disc brown, or grey to black, ±dull, often pruinose | 3 |
| 2(1) | Margin partly brown in section; periphysoid layer loose, strongly gelatinized; periphysoids parallel, sparingly branched and with comparatively narrow lumina | <i>Stictis brunescens</i> |
| | Margin colourless in section; periphysoid layer compact, not strongly gelatinized; periphysoids intricately branched and with comparatively wide lumina..... | <i>Stictis radiata</i> |
| 3(1) | Periphysoids ±distinct; margin in section with prominent and abundant crystals..... | 4 |
| | Periphysoids absent or indistinct; margin in section without, or with only a few crystals | 6 |
| 4(3) | Ascospores less than 3 µm broad | <i>Stictis mollis</i> |
| | Ascospores more than 3 µm broad..... | 5 |
| 5(4) | Periphysoids intricately branched, terminal cells never elongated..... | <i>Stictis populorum</i> |
| | Periphysoids parallel, unbranched or only slightly branched, terminal cells usually elongated | <i>Stictis confusum</i> |
| 6(3) | Proper epithecium (tips of paraphyses) very thick and conspicuous; asci > 200 µm long; disc black, non-pruinose, or the pruina never forming a thick layer | <i>Schizoxylon albescens</i> |
| | Proper epithecium (tips of paraphyses) inconspicuous if at all present; asci < 150 µm long; disc black but usually covered by a thick grey pruina | <i>Carestiella socia</i> |

Taxonomy

Carestiella socia Bres., *Malpigia* 11: 274 (1897).

(Figs 2L, 4)

Type: **Italy:** Valseria, 1863, *Carestia* (S—lectotype; S—isolectotype).

Stictis curtispora Dearn. & Bisby, *Fungi Manitoba* 64 (1929).

Type: **Canada:** Manitoba: Winnipeg, 1926, Bisby 2610 (DAOM—isolectotype).

?*Stictis schizoxylodes* Ellis & Everh., *Proc. Philadelphia Acad. Sci.* 46: 150. (1894).

Type: **USA:** Montana: Sheridan (CUP—isolectotype *vide* Sherwood, not seen).

A saprotrophic fungus on *Populus* twigs (Fig 2L) and smooth bark; in the latter cases possibly lichenized. *Ascomata* ca 0.5–1(–1.7) mm diam. *Margin* dark greyish brown, ±pruinose, particularly in young ascomata, ca (70–)90–120 µm in section, formed by thick-walled brown, widely spaced hyphae with narrow lumina embedded in a gelatinous matrix, lacking crystals entirely; hyphae in the outer part with a vertical orientation, in the inner part often even more widely spaced and pointing toward the hymenium with free ends, adjacent to the hymenium sometimes thin-walled and with larger lumina, which may appear as periphysoids (Fig 4D–F). *Disc* black, but usually covered by a thick grey pruina. *Hymenium* I+ bluish, 80–125 µm; subhymenium 20–30 µm thick. *Paraphyses* olivaceous to brown in the upper part, exceeding the asci by a few micrometers only, but covered by a crystal deposit up to 15 µm thick (Fig 4A); marginal paraphyses indistinct, slightly olivaceous. *Asci* 75–125 × 10–15 µm, with a comparatively well-developed tholus (ca 7–8 µm), (8–)16(–32)-spored. *Spores* ca 30–75(–120) µm, often arranged in two to three coiled bundles (Fig 4B–C).

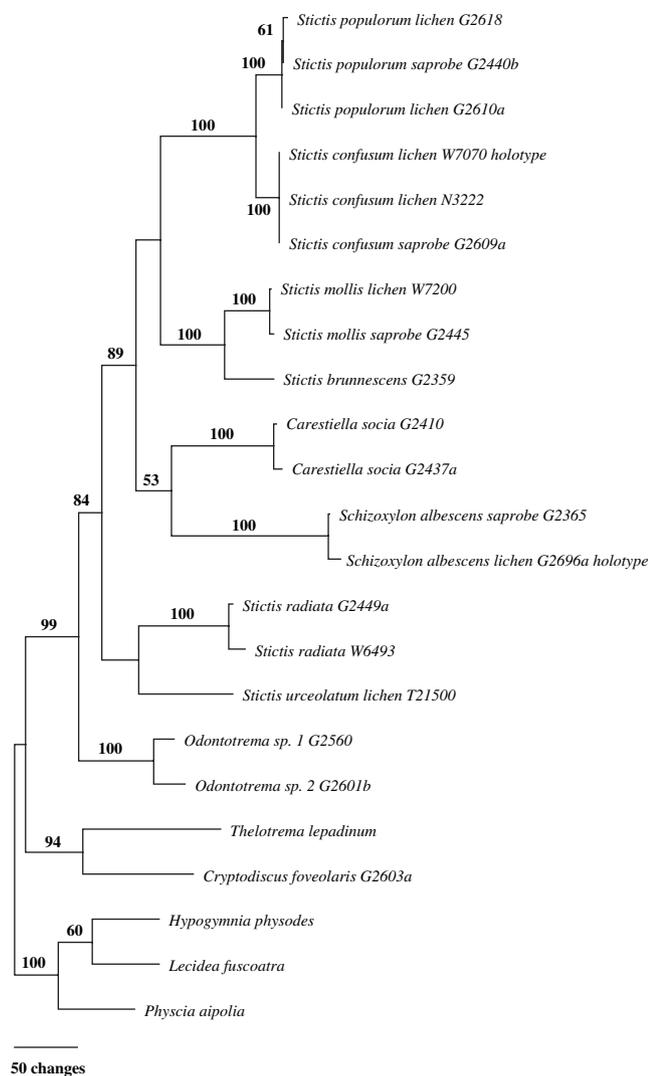


Fig 3 – The single most parsimonious tree (1397 steps, CI = 0.6, RI = 0.7). Branch lengths are proportional to nucleotide changes; jackknife values are given above the branches.

Nomenclatural note. In Herb. Bresadola, housed in S, are two original specimens of *Carestiella socia*. These are obviously parts of the same collection. The fragment annotated and illustrated by Sherwood (1977: 218) is considerably poorer than the other part. Sherwood cited the specimen she investigated as ‘holotype’ apparently unaware of that the original specimen was divided into two duplicates. Art. 9.8 (Greuter et al. 2000) states that this usage of the term ‘holotype’ is an error to be corrected to ‘lectotype’, but that this lectotypification is to be followed. This is somewhat unfortunate as the other is of better quality, but we are forced to accept Sherwood’s lectotypification.

Carestiella is a monotypic genus, which (Fig 3) is nested within *Stictis* s. lat. We believe that retaining *Carestiella* as a separate genus is useful, despite that this causes *Stictis* to become paraphyletic in our very limited phylogeny. It should be noted that this decision is based on the unique and very distinctive anatomical characteristics, and not on any

phylogenetic results. *C. socia* is characterized by the distinct marginal structure of the ascomata, which differs from all other species included here. The hyphae are sparsely interwoven, leaving large areas filled with a gelatinous matrix between the hyphal walls. The polysporous (ca 16 spores) asci are also distinct among the species in our area. Although *C. socia* is also usually characterized by the crystalline pruina on top of the hymenium, this varies considerably in thickness and specimens on dead wood may sometimes be completely devoid of pruina. Such specimens have dark brown to almost black discs. *C. socia* may possibly sometimes be lichenized; we have observed that the ascoma often appear on whitish areas not unlike the ones formed by, e.g. *Stictis mollis* in its lichenized state. We have also occasionally noted algae in sections, including the type of *C. socia*. This requires further study.

S. schizoxylodes is very similar to *C. socia* (fide Sherwood 1977b), particularly in the structure of the ascoma margin, and Wedin et al. (2005) suspected that the names could be synonyms. We have not managed to investigate original material of this name and cannot presently confirm this. We have, however, studied an isotype of *S. curtispora*, which we consider to be the same species as *C. socia*, and which according to Sherwood is conspecific with *S. schizoxylodes*. Sherwood’s drawing of the asci and spores in *Carestiella* has been difficult to verify in the type material investigated. We have not been able to find asci with as many and distinctly small spores as she illustrates.

C. socia was reported from Sweden (as *S. curtispora*) by Gilenstam (1969).

Known localities: Sweden: Lycksele Lappmark: Lycksele par., Furu-
vik, (18°41’E, 64°35’N) 2001 Gilenstam 2410, 2473a, 2491b, 2549; Stensele par., Lake Storuman, SE of Mt Kyrkberget, (65°16’N, 16°49’E) 2002 Wedin 7073; Lule Lappmark: Jokkmokk par., Västigården, (66°45’N, 19°20’E) 2000 Gilenstam 2360; Randijaur, Palotevva, (66°45’N, 19°20’E) 2001 Gilenstam 2437a, 2437b, 2437c, 2441b; Björkholmforsen, (66°45’N, 19°00’E) 2004 Gilenstam 2660a, 2663b; Nau-tijaurälven, (66°50’N, 19°00’E) 1964, Gilenstam 1032 (UPS, filed under *S. populorum*). **Norway:** Troms: Storfjord, ca 6 km SE Skibotn, at Tromsø University Field Station, (69°21’N, 20°22’E) 2003 Wedin 7192, 7194.

Schizoxylon albescens Gilenstam, Döring & Wedin, sp. nov.

(Figs 2A–C, 5)

Etym.: ‘albescens’, meaning ‘whitish’, referring to the colour of the colonies of the lichenized morph.

Similis Sch. alboatri, sed differt ascis et sporis parvioribus, et crystallis paucioribus.

Typus: **Sweden:** Lycksele Lappmark: Lycksele par., Lycksbäcken (64°38’N, 18°38’E), on the trunk of *Populus tremula* along the stream, 14 May 2005, Gilenstam 2696a (UPS-holotypus; K(M)-isotypus).

‘*Schizoxylon* sp 1’, ‘*Schizoxylon* sp 2’ Wedin et al. (2005).

DNA sequences originating from the holotype (GenBank accession numbers): DQ401144 nuclear ITS and LSU rDNA; DQ401142 mitochondrial SSU rDNA.

A saprotrophic fungus (Fig 2C) on dead, decorticated twigs and branches of *Populus tremula*; or as a lichen (Fig 2A–B) on bark of *Populus*, forming distinct bright white thalli, usually in and around deep cracks in the bark. Ascomata ca 1–2 mm wide (saprotroph) or ca 0.5–1 mm (lichenized morph) in diam. Margin greyish brown to white, pruinose, ca 80–125 µm in section, lacking crystals within or with a few scattered crystals; composed of an outer layer including

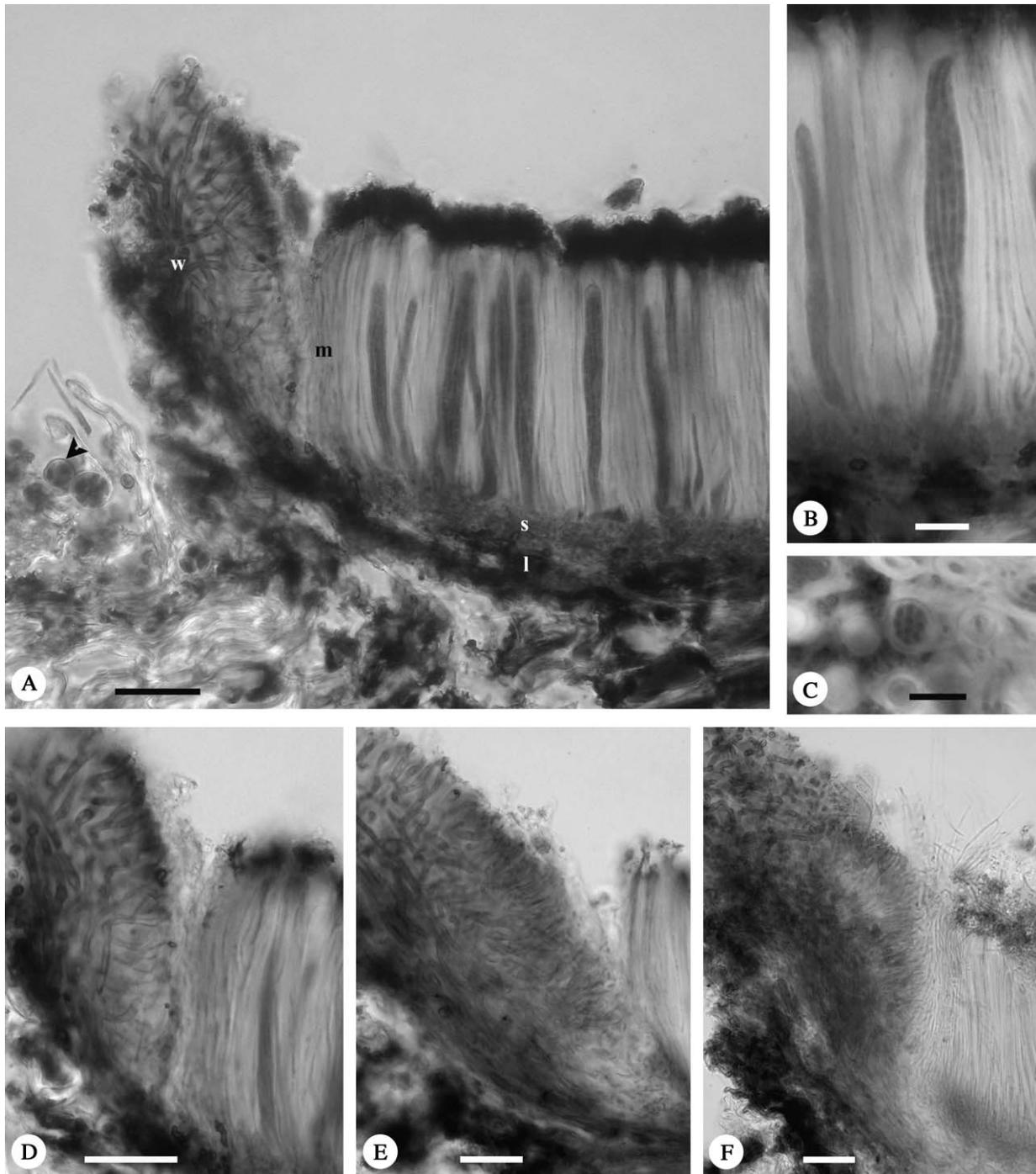


Fig 4 – *Carestiella socia*. (A) Ascoma with crystalline deposit on the hymenium and thin hypothecium/lower ascoma wall beneath the subhymenium; note algae (arrowhead) on substrate next to the ascoma. (B) Ascus with two twisted bundles of spores. (C) Ascus in transverse section showing at least ten individual spores. (D) Ascoma wall with widely spaced hyphae, but lacking periphysoids. (E) Outer wall with thin-walled, periphysoid-like hyphae close to the hymenium. (F) Outer wall dominated in the lower part by thin-walled hyphae resembling periphysoids. Specimens: A, B, D = Wedin 7192; C = Gilenstam 2360; E = Gilenstam 2663a; F = Gilenstam 2441b. l, Hypothecium/lower ascoma wall; m, marginal paraphyses; s, subhymenium; w, true ascoma wall. Bars: A = 30 μm ; B, C = 10 μm ; D–F = 20 μm .

remnants of host tissue, and a major inner layer of hyaline interwoven hyphae, with some pigmentation in the upper part (Fig 5A–D); the inner layer continues below the subhymenium forming a hyaline hypothecium/lower ascoma wall;

periphysoids absent. Disc \pm plane, in older ascomata often somewhat cupulate, black, smooth to granulose, occasionally somewhat pruinose. Hymenium I+ bluish, ca 250–450 high; subhymenium ca 20–30 μm high. Epithecium prominent,

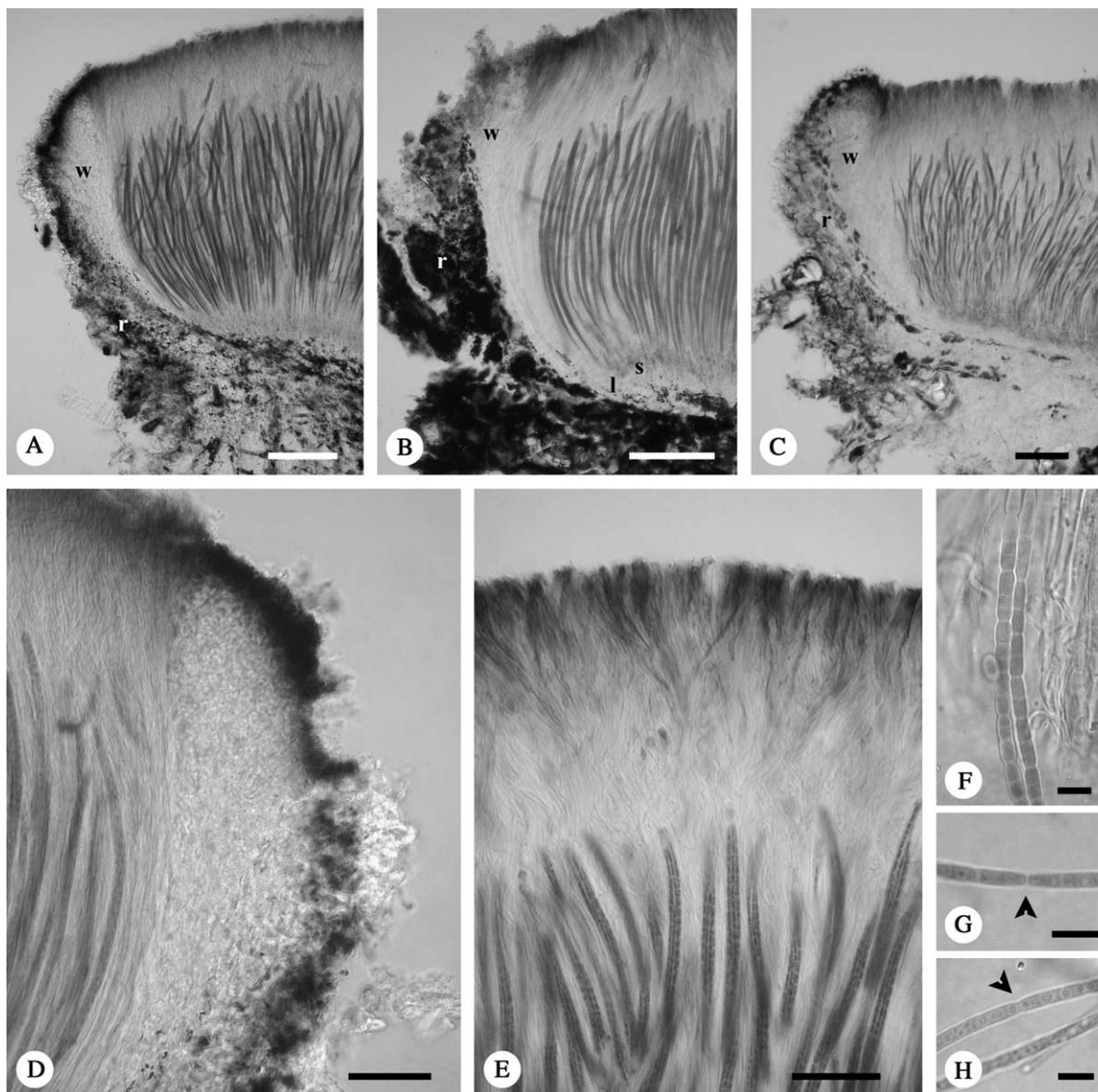


Fig 5 – *Schizoxylon albescens*. (A) Ascoma with pigmented surface of the proper ascoma wall and hardly any involvement of host tissue. (B) Ascoma surrounded by host tissue, proper wall only very faintly pigmented. (C) Ascoma partly embedded in host tissue and pigmentation of the upper surface of the proper ascoma wall only. (D) Detail of the proper ascoma wall; note the lack of periphysoids and of marginal paraphyses in the adjacent hymenium. (E) Epithecium formed by coloured, interwoven tips of paraphyses. (F) Regularly constricted spores. (G–H) Spore with constriction at a septum (arrowhead). Specimens: A, D, G, H = Gilenstam 2443a (saprotrophic morph); B, E = Gilenstam 2434 (saprotrophic morph); C = Wedin 7345 (lichenized morph); F = Wedin s.n., Norrfors 2004 (lichenized morph). l, Hypothecium/lower ascoma wall; r, remnants of host tissue; s, subhymenium; w, proper ascoma wall. Bars: A–C = 100 μ m; D, E = 40 μ m; F–H = 5 μ m.

formed by the branched and interwoven tips of paraphyses, exceeding the asci with ca 60–150 μ m (Fig 5E); no marginal paraphyses differentiated. Asci ca 200–280 (–400 when protruding through the epithecium) \times 8 μ m; 8-spored. Spores ca 150–270 \times 1.5–2.5 μ m, often \pm coiled within the asci, usually with several prominent constrictions at septa (Fig 5F–H), some eventually breaking apart at these after discharge, forming 2–15-septate spore fragments. It is extremely difficult to measure the spores accurately in this species. *Phycobiont*: an unidentified coccoid green alga with rounded cells, ca 6–8 μ m in diam.

This species is referred to as *Schizoxylon*, as it shares important characters with this genus (the absence of periphysoids, and the distinct epithecium formed by the tips of the paraphyses; Sherwood 1977a, 1977b). *Schizoxylon* is a morphologically well-characterized group, which in our phylogenies is nested within *Stictis* s. lat. (Fig 3). We believe that it is useful to acknowledge the distinctive morphological characteristics that currently distinguish *Schizoxylon* from *Stictis*. The retention of *Schizoxylon* as a separate genus here is thus based on the distinctive morphology only and not on any phylogenetic

results, but we note that, with our admittedly very limited sampling, *Stictis* becomes paraphyletic. *S. sepincola*, the type species of *Schizoxylon*, was not included in the investigation by Wedin et al. (2005) and further investigations of the delimitation of *Schizoxylon* versus *Stictis* are clearly needed.

S. albescens is a common epiphyte on *Populus tremula*. The holotype represents the lichenized morph, which is often visible at a distance as distinct white patches on the trunks. *S. albescens* is, apart from the large epithecium and lack of periphysoids, distinguished from the other taxa in our area by having ascomata where the disc and margin are of the same height (Fig 5A–C). Ascomata are often rather scarce. The otherwise similar *S. alboatrum* (not known from our area) differs in having larger asci and spores, and in having a large amount of crystals in the ascoma margin. The apothecial disc is also reported to be glossy in *S. alboatrum*. The material of *S. alboatrum* reported by Gilenstam (1969) belongs to *S. albescens*. We have often observed that some spores of *S. albescens* break in the preparations, and that the spores usually have constrictions (Fig 5F–H) where these breaks apparently occur. However, this seems not to happen when the spores are within the asci.

For a long time, we interpreted the saprotrophic and lichenized specimens as belonging to separate species (e.g. in Wedin et al. 2005), but we now interpret this as an additional example of a species showing optional lichenization. Saprotrophic specimens are often somewhat larger than lichenized samples, but this is in line with other taxa showing optional lichenization.

Known localities: **Saprotrophic morph:** **Sweden:** *Jämtland:* Rätan par., Sörtjärn (62°20'N, 14°38'E), 2004 Wedin 7575, 7576; *Lycksele Lappmark:* Lycksele par., Furuвик (64°34'N, 18°40'E) 2001 Gilenstam 2434; as above, 2004 Gilenstam 2689; *Bocksliden*, (64°35'N, 18°41'E) 2002 Gilenstam 2523b, 2635b; *Tärna par., Klippen* (65°51'N, 15°01'E) 2002 Wedin 7020; *Lake Stor-Björkvattnet, Fräkenviken* (65°36'N, 15°15'E), 2002 Wedin 7034, Gilenstam 2534a; *Åmsele par., Mårdseleforsarna* (66°35'N, 19°25'E), 2001 Gilenstam 2471; *Lule Lappmark:* Jokkmokk par., Randijaur, Västigården (19°20'E, 66°45'N), 2000 Gilenstam 2361; *Palotevva* (19°20'E, 66°45'N), 2001 Gilenstam 2443a; *Björkholmforsen* (19°00'E, 66°48'N), 2000 Gilenstam 2365; as above, 2004 Gilenstam 2660b, 2662a.

Lichenized morph: **Sweden:** *Västmanland:* Tärnsjö par., Tinäset Nat. Res., Bergaholmen (60°08'N, 16°47'E), 1995 Hermansson 4983a (UPS); *Dalarna:* Malung par., Flämtmyren (60°43'N, 13°13'E), 1990 Hermansson 2522 (UPS); *Särna par.:* Brattfjället, Stormorvallens fäbod, (61°34'N, 12°31'E) 1991 Hermansson 2623 (UPS); *Hälsingland:* Forsa par., ca 4.5 km SW Forsa church, Mt Storberget, 2004 Wedin 7593a; *Ångermanland:* Nätra par., Nätra Fjällskog, Västanåhöjden (63°10'N, 18°16'E) 2004 Wedin 7344, 7345; *Nordmaling par., Nyåker*, (63°45'N, 19°18'E), 2003 Wedin 7104; *Norrfors* (63°45'N, 19°00'E), 2004 Wedin s.n.; *Västerbotten:* Umeå, Tjälamark (63°52'N, 20°12'E), 2002 Wedin 6986; as above, 2004 Wedin 7605; *Norrbottnen:* Boden par., Kusträsk (21°45'E, 65°30'N), 2001 Gilenstam 2479; *Pajala par., N of Pajala* (67°13'N, 23°19'E), 2004 Ihlen 1473 (UPS); *Lycksele Lappmark:* Malå par., ca 4 km NNE Grundträsk, along river Skellefteälven (64°11'N, 19°20'E), 2002 Wedin 6869; *Lycksele par., Granträsk*, (64°15'N, 18°15'E), 2002 Gilenstam 2552; *Lycksele, Furuвик* (64°34'N, 18°40'E), 2000 Gilenstam 2352, 2354, 2374, 2382, 2383, 2387, 2399; as above, 2001 Gilenstam 2409, 2447, 2453, 2454, 2462, 2463, 2464a, 2466, 2485, 2486, 2490, 2493, Wedin 6735, 6737, 6742; as above, 2003 Gilenstam 2517; as above, 2004 Gilenstam 2667, 2676; *Tannberget*, 2000 Gilenstam 2369, 2390; *N of Kattisavan, c. 300 m. E of Fräkengård*, 1997 Ahlberg (UME); *Lycksbäcken*, 2005 Gilenstam 2691, 2696b;

Åmsele par., Mårdseleforsarna (66°35'N, 19°25'E), 2001 Gilenstam 2469; *Stensele par., Lake Storuman*, 5 km NNW Storuman, W Mt Surnäsberget (65°08'N, 17°06'E), 2002 Wedin 7077, 7078; *Lake Storuman, SE Mt Kyrkberget* (65°26'N, 16°48'E), 2002 Wedin 7075; *Lake Umnässjön*, 2 km SW Forsnacken (65°26'N, 16°29'E), 2002 Wedin 7065; *Lake Umnässjön, Hällnäs* (65°28'N, 16°00'E), 2002 Wedin 7067; *Tärna par., Lake Stor-Björkvattnet, S of Grukkeluokte* (65°36'N, 15°10'E) 2002 Wedin 7023; *Lake Stor-Björkvattnet*, 2 km SE Fräkenvik, 2002 Wedin 7026b, 7027, 7028; *Fräkenviken* (65°36'N, 15°15'E), 2002 Wedin 7030, Gilenstam 2533a, 2534, 2536; *Lake Gäuta, Forsvik, W of Mt Gäutaberget* (65°39'N, 15°27'E), 2002 Wedin 7035, 7036; *Lule Lappmark:* Jokkmokk par., Köpenhamn (66°55'N, 17°50'E), 2001 Gilenstam 2448b; *Björkholmforsen*, 66°48'N, 19°00'E, 2000 Gilenstam 2367; as above, 2001 Gilenstam 2451b; as above, 2003 Gilenstam 2616, 2622; **Norway:** *Troms:* *Storfjord*, ca 7.5 km SSE Skibotn, W of Brennfjellet (69°19'N, 20°21'E), 2003 Wedin 7199.

Material of *Schizoxylon alboatrum* investigated for comparison: **Germany:** *Bavaria:* Windsheim, Rehm [Rehm, Ascomyceten 478] (UPS—isotype). **Greece:** Attika, Pentelikon, 1971 Poelt (GZU).

Stictis Pers., *Obs. Mycol.* 2: 73 (1799).

Stictis is most likely a paraphyletic group, where the species treated here differ from *Schizoxylon* and *Carestiella* by having a distinct periphysoidal layer, and by lacking part-spores or a thick epithecium.

***Stictis brunnescens* Gilenstam, Döring & Wedin, nom. nov.**

(Figs 2F, 6A–C)

Etym.: 'brunnescens', meaning 'somewhat brownish' is referring to the pigmentation in the ascoma margin.

Basionym: *Stictis mollis* ssp. *populorum* Sherwood, *Mycotaxon* 5: 214 (1977).

Type: **Finland:** *Lapland:* Inari, by the river Kaamasjoki, on *Populus tremula*, Ahti 29717 (H—holotype).

Non *S. populorum* (Gilenstam) Gilenstam, in Wedin et al., *Lichenologist* 37: 74 (2005).

'*Stictis* aff. *mollis* ssp. *populorum*' Wedin et al. (2005).

A saprotrophic fungus (Fig 2F), growing on decorticated wood and twigs of *Populus tremula* and *Salix caprea*. It has also been collected on *Sorbus aucuparia* (Finland, Vuorijärvi, 1937 Laurila, H). Ascomata ca 0.5–1 mm in diam. Margin white, pruinose, entirely encrusted in crystals, ca 50–125 µm in cross section, 4-layered with (1) an outermost layer including remnants of host tissue, (2) a proper outer wall layer of hyaline hyphae, not well-delimited from (3) the crystalliferous layer where crystals are ±abundant particularly in the upper part, and (4) a periphysoid layer, 40–50 µm thick, formed by sparsely branched, strongly gelatinized hyphae with a comparatively narrow lumen (Fig 6A–B). In section, a brown-pigmented area, where an amorphous pigment is deposited in varying amounts, can be observed at the base of the margin. Disc ochraceous, smooth, glossy, non-pruinose. *Hymenium* I+ pale bluish, ca 175–250 µm high; *subhymenium* ca 25–40 µm thick. Paraphyses not exceeding the asci, no epithecium formed; marginal paraphyses very faintly pigmented, connected to the hypothecium/lower ascoma wall layer, surrounding the subhymenium (Fig 6C). The hypothecium/lower ascoma wall layer is formed by hyphae, which are in connection with the marginal paraphyses and also to the proper outer wall layer. Asci ca 175–250 × 6–8 µm. Spores ca 160–245 × 2 µm.

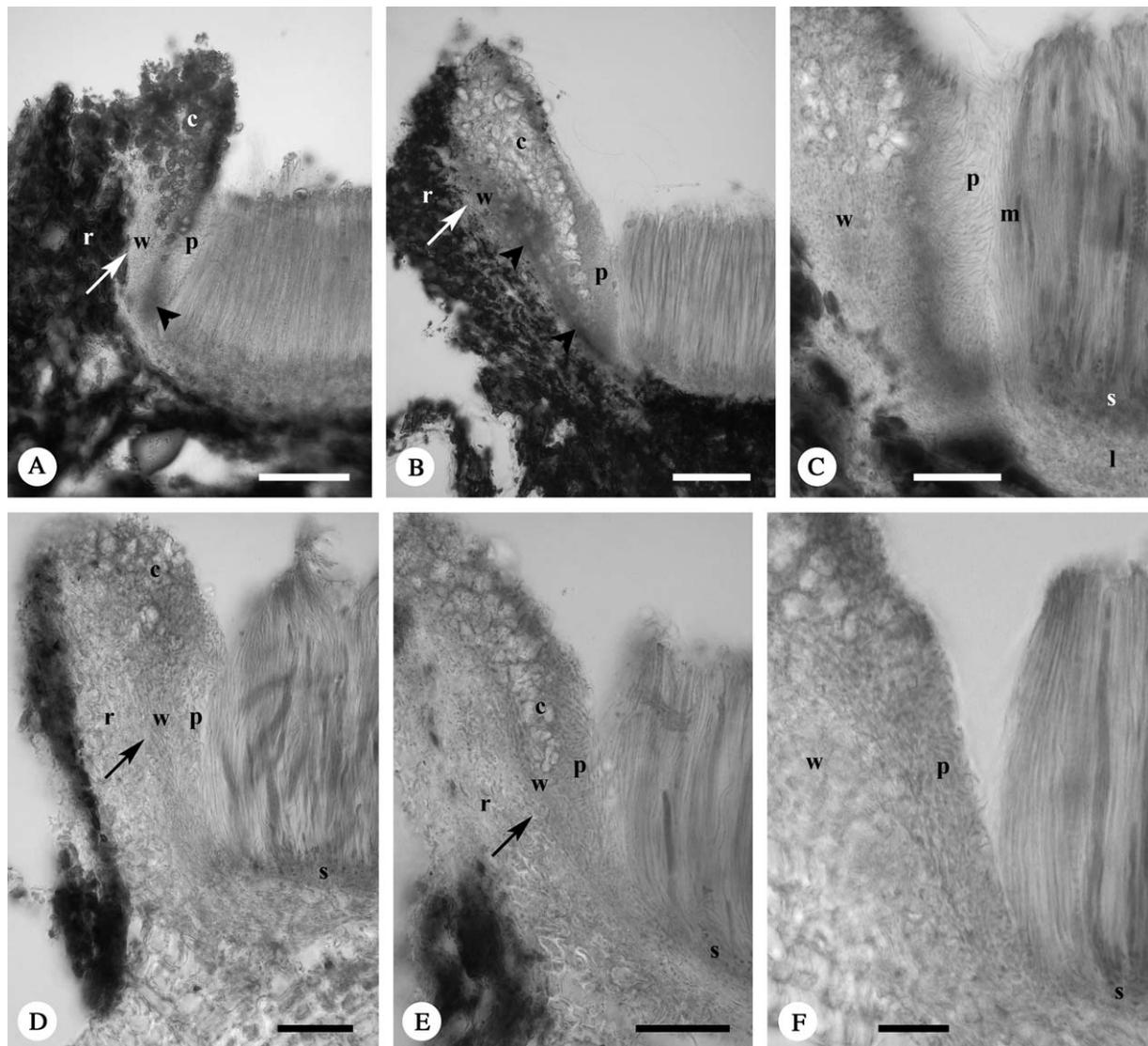


Fig 6 – (A–C) *Stictis brunnescens*. (A) Ascoma with brownish pigmentation at the base of the ascoma margin next to the periphysoid layer (arrowhead); section in water. (B) Ascoma with brownish pigmentation at the lower outer side of the proper ascoma wall (arrowheads). (C) Details of the ascoma margin, pigmentation behind the periphysoid layer; note very faintly pigmented marginal paraphyses in connection with the hypothecium/lower ascoma wall. (D–F) *S. radiata*. (D) Unpigmented ascoma with crystals in the upper margin and a layer including remnants of host tissue. (E) Ascoma with a prominent crystalliferous layer. (F) periphysoids. Specimens: A, C = Gilenstam 2614; B = Gilenstam 2538; D–F = Gilenstam 2449a. c, Crystalliferous layer; l, hypothecium/lower ascoma wall; m, marginal paraphyses; p, periphysoids; r, remnants of host tissue; s, subhymenium; w, proper ascoma wall; arrow indicates boundary between proper ascoma wall and host tissue. Bars: A, B = 100 μ m; C–E = 50 μ m; F = 25 μ m.

Stictis brunnescens is habitually similar to *S. radiata* in the distinctly ochraceous, glossy ascoma disc and white pruinose margin, but differs by having at least some brown pigmentation in the otherwise colourless proper margin, in having straight, sparsely branched, strongly gelatinized periphysoids, and in the presence of marginal paraphyses. Sherwood (1977a) introduced the name *S. mollis* ssp. *populorum* for this taxon, which is not particularly similar to *S. mollis* in habit or anatomy, despite forming sister groups in our analyses (Fig 3; Wedin et al. 2005, fig. 2). We have studied the type and some additional material verified by Sherwood, which is clearly

the same as our species. As the epithet *populorum* is already used on species level in *Stictis*, we here introduce the new name *S. brunnescens* for this distinct fungus.

Known localities: Sweden: Hälsingland: Forsa par., ca 4.5 km SW Forsa church, Mt. Storberget (61°53'N, 16°42'E), 2004 Wedin 7594; Lycksele Lappmark: Tärna par., Lake Övre Boksjön, S Mt. Nils Erikberget (65°39'N, 15°52'E), 2002 Wedin 7057, Gilenstam 2538; Lycksele par., Furuvik (65°34'N, 18°41'E), 2001 Gilenstam 2412; as above, 2002 Gilenstam 2577, 2598; as above, 2003 Gilenstam 2608, 2614, 2628, 2634, 2637, 2638a; as above, 2004 Gilenstam 2664, 2666; Lycksbäcken, 2005 Gilenstam 2692, 2693; Lule Lappmark: Jokkmokk par., Randijaur, Palotevva (66°45'N, 19°15'E), 2004 Gilenstam 2658;

Björkholmforsen (66°48'N, 19°00'E), 2000 Gilenstam 2359. Finland: Satakunta: Suodenniemi, Kirtankylä, Miekktajärvi, 1936 Laurila (H); Siikainen, Vuorijärvi, 1937 Laurila (H). Russia: Kuusamo: Salla, 1937 Laurila (H).

Sherwood (1977a) also reported this taxon from Norway (on *Ulmus*, Sommerfelt; on *Populus*, 1840 Linderun, O) and from the Swedish province of Småland (Femsjö, Herb. Fries, UPS). We have no reason to doubt these identifications, but have not re-studied this material.

Stictis confusum Gilenstam, Döring & Wedin, sp. nov.

(Figs 1A–B, 2D–E, 7)

Etym.: 'confusum', referring to the difficulty in separating it from the closely related and extremely similar *S. populorum*.

Similis *St. populori*, sed differt periphysoidibus parallelibus et characteribus molecylaribus.

Typus: Sweden: Lycksele Lappmark: Stensele par., Lake Storuman, SE of Mt Kyrkberget, directly after the turnoff towards the village Kyrkberget (65°16'N, 16°49'E), young *Pinus*-forest, on *Populus*, 2002, Wedin 7070 (UPS-holotypus; K(M)-isotypus).

'*Stictis* sp 2' / '*Conotrema* sp 2' Wedin et al. (2004).

DNA sequences originating from the holotype (GenBank accession numbers): DQ401143 nuclear ITS and LSU rDNA; DQ401141 mitochondrial SSU rDNA.

A saprotroph (Fig 2E) on wood of *Populus tremula* or *Salix caprea*, particularly on decorticated branches still remaining on the living trunks, or as a lichen (Fig 2D) in and around cracks in the thick bark on lower parts of the trunks of *Populus* trees, particularly on older trunks. The lichenized morph has a white thallus, in which a very loosely

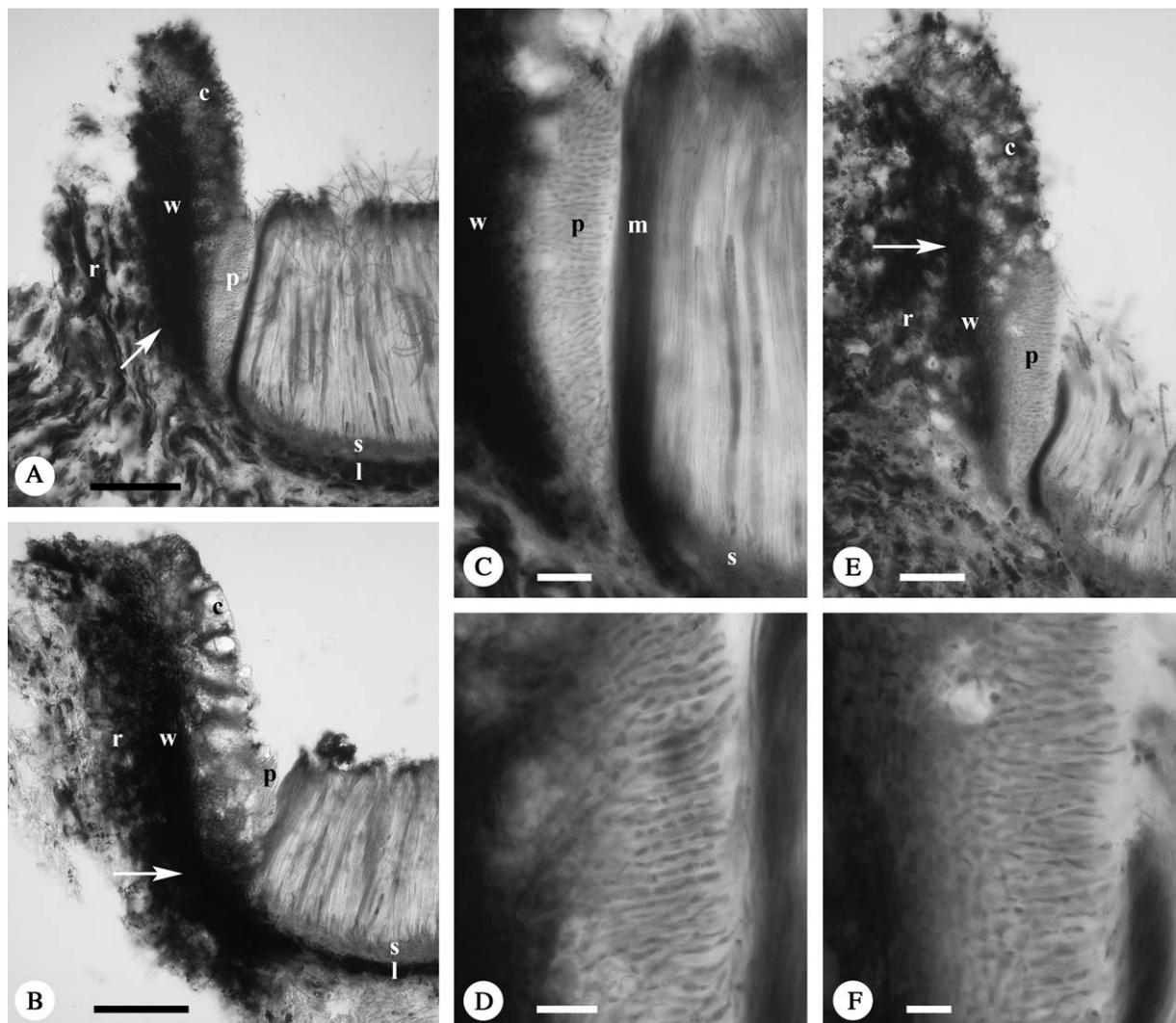


Fig 7 – *Stictis confusum* saprotrophic (A–D) and lichenized (E–F) morphs. (A) Ascogonium surrounded by uncarbonized host tissue. (B) Ascogonium with carbonized wall layers, where the layer including remnants of host tissue is difficult to delimit from the proper outer wall and protrudes below the ascogonium. (C)Periphysoid layer, and dark coloured marginal paraphyses surrounding the subhymenium. (D)Periphysoids in rows of parallel hyphae. (E) Ascogonium embedded in host tissue with carbonized margin. (F)Periphysoids with elongated end cells. Specimens: A, C, D = Gilenstam 2609a; B = Gilenstam 2542a; E, F = Nordin 3222. c, Crystalliferous layer; l, hypothecium/lower ascogonium wall; m, marginal paraphyses; p, periphysoids; r, remnants of host tissue; s, subhymenium; w, proper ascogonium wall; arrow indicates boundary between proper ascogonium wall and host tissue. Bars: A, B = 100 µm; C = 25 µm; D, F = 10 µm; E = 50 µm.

lichenized, unidentified coccoid green algal photobiont is present. Ascomata ca 0.6–1.3 mm in diam (saprotrophic morph) or ca 0.5–0.8 mm in diam. (lichenized morph). Margin grey to white, \pm pruinose, ca (70–)120–160 μ m in cross-section, four layered (Fig 7A–B, E), with (1) an outer layer including remnants of host tissue, and occasionally with scattered algae at the surface in the lichenized morph, an (2) a proper outer wall layer of strongly pigmented, thick-walled hyphae, this second layer and adjacent parts of the first can be strongly carbonized, (3) a prominent crystalliferous layer where crystals are present particularly in the upper part, and (4) a periphysoid layer, ca (30–)40–50 μ m thick, formed by parallel, sparsely branched, hyphae, ca 2–4 μ m wide, the terminal cells often somewhat elongated, up to 4–6 times longer than wide (Fig 7C–D, F). Disc dark brown, often with a grey pruina. Hymenium I+ blue, ca 180–250 μ m high; subhymenium 20–30 μ m high. Paraphyses hyaline, with a very light brown pigmentation in the uppermost parts, no distinct epithecium formed but the tips covered with some crystals; marginal paraphyses distinctly brownish, connected to the hypothecium/lower ascoma wall layer, surrounding the subhymenium. The hypothecium/lower ascoma wall layer is formed by hyphae, which are in connection with the marginal paraphyses and also to the proper outer wall layer (Fig 1A–B). Asci ca 180–230 \times 12–15 μ m. Spores ca 170–220 \times 4–4.5 μ m.

Stictis confusum was not distinguished from *St. populorum* until recently, in a multigene study (Wedin et al. 2004, as *Stictis/Conotrema* sp. 2) where a larger number of specimens from different parts of the distribution area were included. These two species are sister taxa (Fig 3), and cannot be distinguished in the field. Although genetically distinct in all four genetic markers investigated by Wedin et al. (2004) they differ only very subtly in anatomy in the structure of the periphysoid layer. *Stictis populorum* has distinctly branched and interwoven periphysoids formed by cells, which are about 2–3(–4) times longer than wide (Fig 9B–D, F). The periphysoids in *S. confusum* are usually only sparsely branched, arranged in more or less parallel rows and the cells towards the end are usually somewhat elongated, up to 4–6 times longer than wide (Fig 7C–D, F). These details are, however, often difficult to observe, as it usually requires well-developed fruit bodies and accurate transverse microtome sections. In lichenized specimens, the periphysoid layer is also usually rather poorly developed, which further complicates the identification. *S. confusum* is, when growing as a lichen, found on large to medium-sized *Populus* trunks, and on dead branches and twigs of *Populus* or *Salix caprea* when growing as a saprotroph. The type specimen is a typical lichenized sample, growing on a comparatively thin *Populus* in an ordinary young *Pinus*-forest.

The specimen Gilenstam 2353 (UPS) used to provide DNA sequences to represent '*Conotrema*' *populorum* by Lumbsch et al. (2004; e.g. AY300833 and AY300882) belongs to *S. confusum*.

Known localities: **Saprotrophic morph:** **Sweden:** Lycksele Lappmark: Stensele par., Kyrkberget (65°30'N, 16°60'E), 2002 Gilenstam 2542a; Lycksele par., Furuviik (65°35'N, 18°40'E), 2001 Gilenstam 2413, 2420; as above, 2003 Gilenstam 2609a; as above, 2004 Gilenstam 2647b.

Lichenized morph: **Sweden:** **Dalarna:** Hamra par., Mt Harjamägg, ca 10 km WSW of Lillhamra (61°37'N, 14°35'E), 1993 Nordin 3233 (UPS); Los par., Mt. Lillkullen, 10 km NE of Rullbo (61°48'N,

14°48'E), 1993 Nordin 3222 (UPS); **Jämtland:** Rätan par., Vitvattnet, 62°21'N, 14°36'E, 2004 Wedin 7583; **Västerbotten:** Umeå, Sörfors, along river Umeälven (63°53'N, 20°03'E), 2005 Wedin 7632; Teg par., Mt Degerberget, S of Lake Degersjön (63°48'N, 20°00'E), 2002 Wedin 6975; **Vindeln par.,** Mt Vorrberget (64°11'N, 19°37'E), 2002 Wedin 6992; **Lycksele lappmark:** Tärna par., Lake Stor-Björkvattnet, Fräkenviken (65°36'N, 15°15'E), 2002 Wedin 7033; Lake Övre Boksjön, S Mt. Nils-Eriksberget (65°39'N, 15°52'E), 2002 Wedin 7051, 7053, 7056, Gilenstam 2537; **Stensele par.,** Lake Storuman, parking area W of Mt. Surnäsberget (65°08'N, 17°06'E), 2002 Wedin 7079, 7081; Lake Storuman, SE of Mt Kyrkberget (65°16'N, 16°48'E), 2002 Wedin 7071, 7074; Lake Umnässjön, 2 km SW Forsnacken (65°26'N, 16°29'E), 2002 Wedin 7063; Lake Nedre Boksjön, Storskog (65°38'N, 15°58'E), 2002 Wedin 7059, 7061, 7062; **Lycksele par.,** Norrás, at Norråstorpet (64°34'N, 18°44'E), 2001 Wedin 6741, Gilenstam 2467; **Gammplatsen,** 2005 Gilenstam 2668; **Tannberget,** 2000 Gilenstam 2353, 2357; **Tannbergsskolan,** 2001 Gilenstam 2401; **Furuviik** (65°34'N, 18°41'E), 2001 Gilenstam 2459, 2627; **Åmsele par.,** Mårdseleforsarna (66°35'N, 19°25'E), 2001 Gilenstam 2472.

Stictis mollis Pers., *Myc. Eur.* 1: 337 (1822).

(Figs 1C–D, 2J–K, 8)

Type: **Europe:** locality unknown (L-Persoon 910.264-828-not seen).

'*Stictis* sp 1/*Conotrema* sp 1' Wedin et al. (2004).

'*Stictis* aff. *mollis*/*Conotrema* sp 1' Wedin et al. (2005).

A saprotroph (Fig 2K) on thin dead branches or twigs of *Populus tremula* or *Salix caprea*, or as a lichen (Fig 2J) on young, thin smooth-barked *Populus*-trunks; also known from other types of wood. The lichenized morph forms small greyish patches, in which a very loosely lichenized, unidentified coccoid green algal photobiont is present, scattered around the ascomata (Fig 1D). Ascomata ca 0.4–0.8(–1.7) mm (saprotrophic morph) or 0.2–0.4 mm (lichenized morph) in diam. Margin grey–white, \pm pruinose, ca 75–120 μ m (saprotrophic morph) or ca 80–100 μ m (lichenized morph) in cross-section, four layered (Figs 1D, 8A, C), with (1) an outer layer including remnants of host tissue, and occasionally with scattered algae at the surface in the lichenized morph, (2) a proper outer wall layer of strongly pigmented, thick-walled hyphae, this second layer and adjacent parts of the first can be strongly carbonized, (3) a crystalliferous layer not well delimited from the second layer, the crystals are scattered particularly in the upper part, and (4) a periphysoid layer, ca 40–50 μ m (saprotrophic morph) or ca 10–30 μ m (lichenized morph) thick, formed by gelatinized, branched hyphae, which in the lichenized morph may be almost indistinguishable (Fig 8B, D). Disc brownish, often with a greyish pruina. Hymenium I+ bluish, ca 120–190 μ m high; subhymenium ca 10–20 μ m. Paraphyses hyaline, not forming a distinct epithecium but with a olivaceous amorphous pigmentation in the uppermost parts; marginal paraphyses not strongly agglutinated, olivaceous, connected to the hypothecium/lower ascoma wall layer, surrounding the subhymenium. The hypothecium/lower ascoma wall layer is formed by hyphae, which are in connection with the marginal paraphyses and also to the proper outer wall layer (Figs 1C, 8E, F). Asci ca 120–190 \times 8–12 μ m. Spores ca 120–180 \times 2 μ m.

Stictis mollis is one of the three *Stictis*-species recently shown (Wedin et al. 2004, as *Stictis* sp. 1/*Conotrema* sp. 1) to be able to live both as a saprotroph on wood, and as a lichen

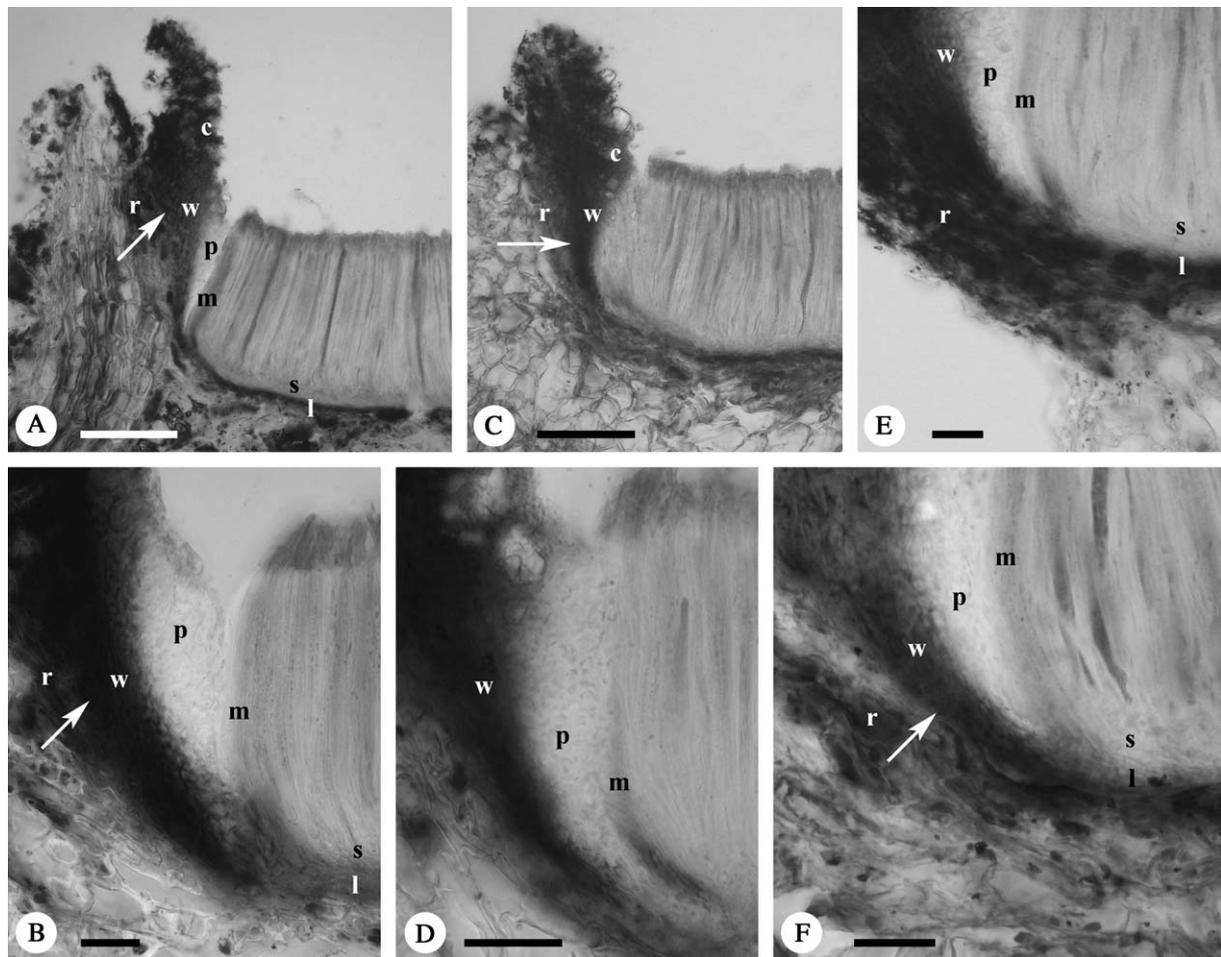


Fig 8 – *Stictis mollis* saprotrophic (A–B) and lichenized (C–F) morphs. (A) Ascoma with slight carbonization of host tissue and well pigmented lower ascoma wall and marginal paraphyses. (B) Periphysoids, and connection of hypothecium/lower ascoma wall with the marginal paraphyses and proper ascoma wall. (C) Ascoma with carbonization of host tissue, but faintly pigmented lower ascoma wall and marginal paraphyses. (D) Periphysoids. (E) Hypothecium/lower ascoma wall in connection with the marginal paraphyses and proper outer ascoma wall with carbonization of host tissue below the edge of the ascoma. (F) Hypothecium/lower ascoma wall in connection with the marginal paraphyses and proper outer wall with rather faint pigmentation. Specimens: A = Wedin 7209; B = Wedin 7024; C–E = Gilenstam 2451a; F = Wedin 7609. c, Crystalliferous layer; l, hypothecium/lower ascoma wall; m, marginal paraphyses; p, periphysoids; r, remnants of host tissue; s, subhymenium; w, proper ascoma wall; arrow indicates boundary between proper ascoma wall and host tissue. Bars: A, C = 100 μ m; B, D–F = 30 μ m.

on bark ('optional lichenization'). We have not investigated material from outside northern Scandinavia (apart from a few specimens verified by Sherwood), and very little on other substrates than *Populus tremula* or *Salix caprea*, but our saprotrophic material fits Sherwood's concept of *St. mollis* very well. Although the lichenization clearly is weak, colonies on aspen bark all seem to be associated with coccoid green algae to some extent.

The amount of brownish pigmentation and carbonization in the ascomatal wall varies considerably, both in the margin and in the lower wall. Particularly in saprotrophic specimens that have been growing in exposed situations, the wall may be strongly carbonized. *S. mollis* is easily distinguished from the two other *Stictis* species with distinctly brown margins, *S. confusum* and *S. populorum*, by the comparatively narrow

spores and the olivaceous, amorphous pigmentation of the uppermost part of the paraphyses.

Known localities: Saprotrophic morph: Sweden: Hälsingland: Enånger par., ca 8 km NW Långvinds Bruk, Ö Myra (61°30'N, 17°00'E), 2004 Wedin 7598, 7599, 7600, 7603; **Jämtland:** Rätan par., Sörtjärn (62°20'N, 14°38'E), 2004 Wedin 7574; Sörtjärn (62°21'N, 14°36'E), 2004 Wedin 7580; **Västerbotten:** Teg par., 11 km W of Holmsund, S of Lake Fisksjön (63°41'N, 20°08'E), 2004 Wedin 7614a; Umeå, Tjälamark (63°52'N, 20°12'E), 2004 Wedin 7606; Tavelsjö par., Mt Orrberget (64°07'N, 20°02'E), 2002 Wedin 6999; Överklinten par., River Rickleån, Överklinten, 2004 Gilenstam 2679; **Lycksele Lappmark:** Lycksele par., Furuvik (64°35'N, 18°41'E), 2001 Gilenstam 2408, 2414, 2421, 2423, 2425, 2428, 2429, 2430, 2435, 2445a, 2445b, 2458a, 2458b; as above, 2002 Gilenstam 2489a, 2491a, 2491c, 2492, 2501a, 2521, 2523a, 2526, 2554, 2563a, 2566, 2575, 2576b, 2585b, 2588, 2589, 2592b, 2593, 2596, 2600; as above, 2003 Gilenstam

2604; Åmsele par., Mårdseleforsarna (66°35'N, 19°25'E), 2002 Gilenstam 2514; Stensele par., Lake Storuman, at parking area W of Mt Sumnäsberget (65°08'N, 17°06'E), 2002 Wedin 7082, 7083; Tärna par., Lake Stor-Björkvattnet, S of Grukkeluokte (65°36'N, 15°10'E), 2002 Wedin 7024; Lake Gäuta, Forsvik, W of Mt Gäutaberget (65°39'N, 15°27'E), 2002 Wedin 7039; Lake Övre Boksjön, Kråkberg (65°40'N, 15°43'E), 2002 Wedin 7043; Lule Lappmark: Jokkmokk par., Randijaur, Palotevva (66°45'N, 19°20'E), 2001 Gilenstam 2440c, 2441c; Randijaur, Kurvusudden, 2004 Gilenstam 2617a; Björkholmforsen (66°45'N, 19°00'E) 2004 Gilenstam 2615, 2624; Nautijaurälven, 2004 Gilenstam 2620a; **Norway:** Troms: Storfjord, ca 13.5 km SSE Skibotn, River Skibotnelva, Lappgroa (69°16'N, 20°28'), 2003 Wedin 7226, 7227; ca 7.5 km SSE Skibotn, River Skibotnelva, W of Brennfjellet (69°19'N, 20°21'E), 2003 Wedin 7209.

Lichenized morph: **Sweden:** Hälsingland: Söderhamn par., Hällmyra, 1991 Ågren 20.IV.1991 (UPS); Enånger par., ca 8 km NW Långvinds Bruk, Ö Myra (61°30'N, 17°00'E), 2004 Wedin 7601, 7602; Forsa par., ca 4.5 km SW Forsa church, Mt. Storberget (61°43'N, 16°42'E), 2004 Wedin 7593b, 7595, 7596; ca 8 km WSW Forsa church, Vallavallen (61°43'N, 16°42'E), 2004 Wedin 7591; Jämtland: Marieby par., N Fugelsta (63°07'N, 14°44'E), 2004 Wedin 7571; Ångermanland: Nätra par., Nätra Fjällskog, Västanåhöjden (63°09'N, 18°16'E), 2004 Wedin 7346; Nordmaling par., ca 4 km SSE Agnäs (63°49'N, 19°17'E), 2003 Wedin 7105, 7106, 7108; Västerbotten: Teg par., ca 11 km W of Holmsund, S of Lake Fisksjön (63°41'N, 20°08'E), 2004 Wedin 7613; Umeå, ca 1.5 km SE Gimönäs, W Rödmosamyren (63°47'N, 20°20'E), 2003 Wedin 7109, 7110; ca 1 km SE Gimönäs, Tegelbruksberget (63°47'N, 20°19'E), 2004 Wedin 7618; Mt. Degerberget (63°49'N, 19°59'E), 2002 Wedin 6970; Tjälåmark (63°52'N, 20°12'E), 2004 Wedin 7609; Tavelsjö par., W of Mt Högländsberget (64°03'N, 19°59'E), 2004 Wedin 7617; Sävar par., along Sävar River, Pålböletomten, (63°57'N, 20°23'E), 2003 Wedin 7182; Lycksele Lappmark: Lycksele par., Furu-
vik (64°35'N, 18°40'E) 2001 Gilenstam 2351, 2370, 2379, 2384, 2411, 2417, 2418, 2446; as above, 2002 Gilenstam 2474, 2488, 2494, 2500 2516, 2517, 2518, 2520, 2522, 2546, 2553; Norrås, along the road to Norråstorpet (64°34'N, 18°43'E), 2001 Wedin 6736, 6739; Stensele par., Lake Storuman, SE of Mt Kyrkberget (65°16'N, 16°49'E), 2002 Wedin 7068, 7072 Gilenstam 2543; Lake Umnässjön, Hällnäs (65°28'N, 16°00'E), 2002 Wedin 7066; Tärna par., Lake Stor-Björkvattnet, 2 km SE of Fräkenvik (65°36'N, 15°17'E), 2002 Wedin 7026a; Lake Gäuta, Forsvik (65°39'N, 15°27'E), 2002 Wedin 7038; Forsbäck (65°40'N, 15°30'E), 2002 Gilenstam 2535; Lule Lappmark: Jokkmokk par., Köpenhamn (66°55'N, 17°50'E), 2001 Gilenstam 2448a; Björkholmforsen (66°45'N, 19°00'E), 2001 Gilenstam 2451a; Norrbotten: Boden par., Kusträsk (65°30'N, 21°45'E), 2002 Gilenstam 2477; Pajala par., Pajala (67°13'N, 23°19'E), 2004 Ihlen 1474 (UPS); **Norway:** Troms: Storfjord, ca 7.5 km SSE Skibotn, River Skibotnelva, W of Brennfjellet (69°19'N, 20°21'E), 2003 Wedin 7200; ca 6 km SE Skibotn, Tromsø University Field Station (69°21'N, 20°22'E), 2003 Wedin 7193.

Additional specimens examined (all saprotrophs): **Germany:** Bavaria: Frankonia, Lugenheim, on *Fraxinus*, 1870 Rehm, Rehm Ascomyceten 22 (UPS); **Sweden:** Uppland: Uppsala, on *Acer*, 1884 Romell (UPS); Skokloster, on *Corylus avellana*, 1967 Lundquist 5282 (UPS); Västerbotten: Umeå, Brännland, on *Syringa vulgaris*, 1968 Eriksson (UME).

Stictis populorum (Gilenstam) Gilenstam, in Wedin et al., *Lichenologist* 37: 74 (2005).

(Figs 2G–H, 9).

Conotrema populorum Gilenstam, *Ark. Bot.* 7: 167 (1969).

Type: **Sweden:** Lule Lappmark: Gällivare par., Satisfjäre, Hapakvarats, 1963, Gilenstam 476 (UPS—holotype).

'Stictis sp 3' Wedin et al. (2004, 2005).

A saprotroph on *Populus* wood (Fig 2H), particularly on decorated branches still remaining on the living trunks, or as

a lichen in and around cracks in the bark of *Populus* (Fig 2G), particularly on lower parts of the trunks on older *Populus* trees. The lichenized morph has a white thallus, in which a very loosely lichenized, unidentified coccoid green algal photobiont is present. Ascomata ca 0.5–1 mm (saprotrophic morph) or 0.3–0.6 mm (lichenized morph) in diam. Margin grey–white, pruinose, ca 100–135(–200) µm in section, four layered (Fig 9A, E), with (1) an outer layer including remnants of host tissue, and occasionally with scattered algae at the surface in the lichenized morph, (2) a proper outer wall layer of strongly pigmented, thick-walled hyphae, this second layer and adjacent parts of the first can be strongly carbonized, (3) a prominent crystalliferous layer where the crystals are usually present predominantly in the upper part, and (4) a periphysoid layer, ca 40–60 µm thick, formed by branched and intricate hyphae, the terminal cells not elongated (Fig 9B–D, F). Disc dark brown, often with a grey pruina. Hymenium I+ bluish, ca 180–250 µm high; subhymenium ca 15–30 µm. Paraphyses may exceed the height of the asci with ca 5–10 µm, crystals are deposited on, and a light brown pigmentation is present in the hyphal walls in the upper parts of the paraphyses; marginal paraphyses brown, connected to the hypothecium/lower ascoma wall layer, surrounding the subhymenium. The hypothecium/lower ascoma wall layer is formed by hyphae, which are in connection with the marginal paraphyses and also to the proper outer wall layer (Fig 9B, F–G). Asci ca 160–240 × 12–15 µm. Spores ca 150–230 × 4 µm.

Stictis populorum is currently a red-listed lichen species in Sweden (as '*Conotrema*' *populorum*, Thor & Arvidsson 1999; Gårdenfors 2005). We still cannot say how widespread or common this species is, as our own collecting efforts have been undertaken in a few regions only. However, it is very likely that it is under-collected in other areas, and several sites are actually *Populus*-regeneration on abandoned agricultural land. Conversely, most specimens filed under the name '*Conotrema*' *populorum* in Swedish herbaria, with the exception of Gilenstam's original samples, represent the far more common *Schizoxylon albescens*. The conservation status of all species of *Stictis* s. lat. in the area needs to be re-assessed.

S. populorum was until recently not distinguished from *S. confusum*, and differ only rather subtly in morphology in the structure of the periphysoid layer. *S. populorum* has distinctly branched and interwoven periphysoids compared with the periphysoids in *S. confusum*, which are only sparsely branched, comparatively parallel, and usually with somewhat elongated end cells (compare Fig 9B–D, F with Fig 7C–D, F). However, this is often difficult to observe, requiring well-developed material and very good sections, particularly in lichenized samples where the periphysoids are usually poorly developed.

The lower wall is very poorly pigmented in lichenized morphs, something that caused Gilenstam (1969) to report that '*Conotrema*' *populorum* lacked a wall beneath the hymenium.

Known localities (in addition to Gilenstam 1969): **Saprotrophic morph:** **Sweden:** Västerbotten: Umeå, Tjälåmark (63°52'N, 20°12'E), 2004 Wedin 7607; Lycksele Lappmark: Lycksele, along river Umeälven, 2005 Gilenstam 2647b; Lule Lappmark: Jokkmokk par., Randijaur, Parkijaur (66°40'N, 19°15'E), 2004 Gilenstam 2619; Palotevva (66°45'N, 19°45'E), 2001 Gilenstam 2440b; Björkholmforsen

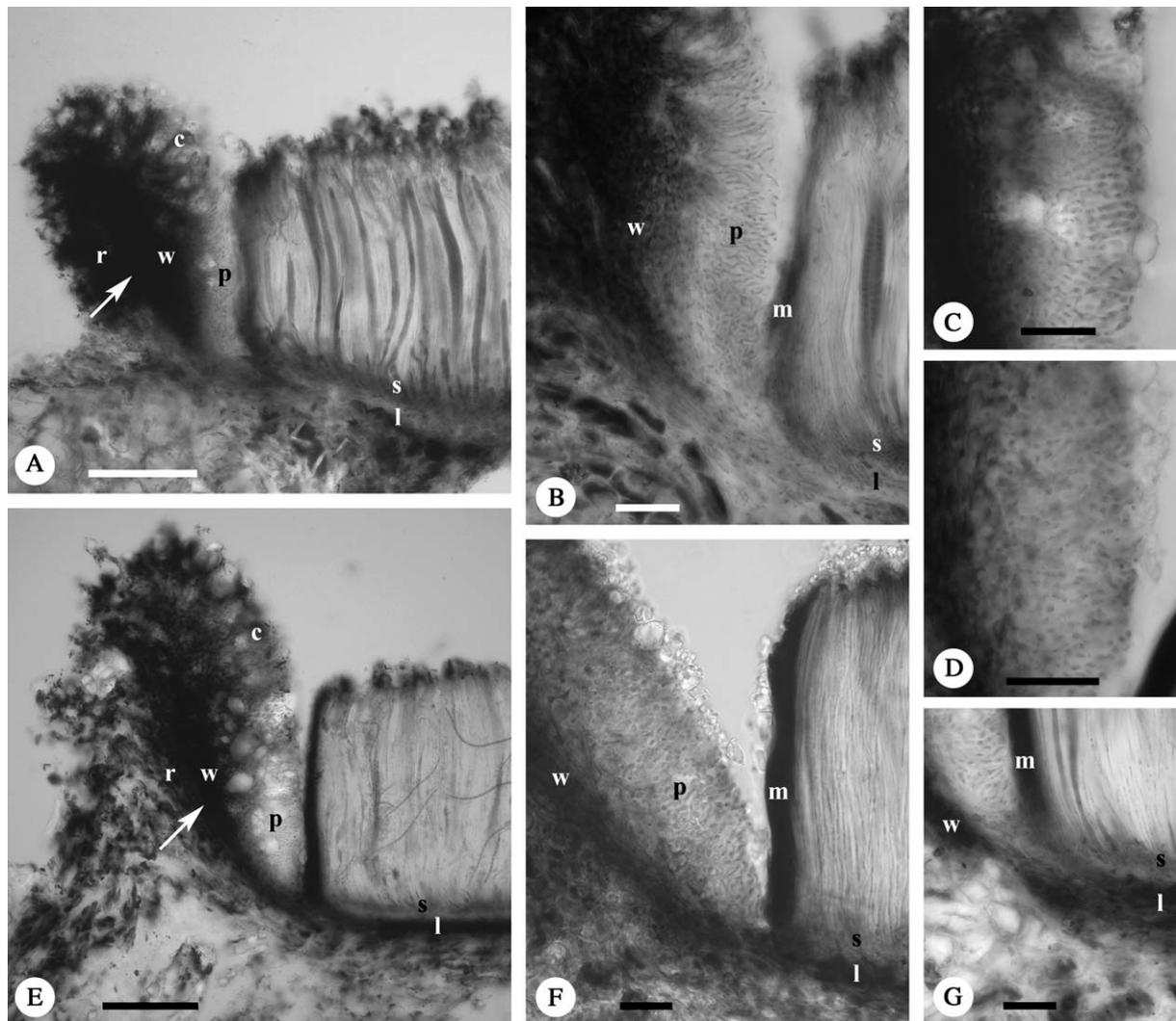


Fig 9 – *Stictis popolorum* lichenized (A–B) and saprotrophic (C–G) morphs. (A) Ascoma with strongly carbonized wall layers, where the layer including remnants of host tissue is hard to delimit from the proper outer wall, hypothecium/lower ascoma wall with an only faintly pigmented hypothecium. (B)Periphysoids and marginal paraphyses connected to an entirely faintly pigmented hypothecium/lower ascoma wall. (C)Periphysoids with rather short cells. (D)Periphysoids formed of interwoven hyphae. (E) Ascoma with strongly carbonized wall layers surrounded by uncarbonized host tissue. (F)Periphysoids and dark coloured marginal paraphyses connected to a strong pigmented hypothecium/lower ascoma wall. (G) Pigmented hypothecium/lower ascoma wall in connection with the marginal paraphyses and the proper outer wall. Specimens: A, B = Nordin 2659; C, E, G = Gilenstam 2619; D, F = Gilenstam 2620b. c, Crystalliferous layer; l, hypothecium/lower ascoma wall; m, marginal paraphyses; p, periphysoids; r = remnants of host tissue; s, subhymenium; w, proper ascoma wall; arrow indicates boundary between proper ascoma wall and host tissue. Bars: A, E = 100 μ m; B–D, F–G = 30 μ m.

(66°45'N, 19°00'E), 2004 Gilenstam 2661, 2663a; Nautijaurälven (66°50'N, 19°20'E) 2004 Gilenstam 2620b; Köpenhamn (6°55'N, 17°50'E) 2001 Gilenstam 2448b.

Lichenized morph: Sweden: Hälsingland: Norrala par., Skallsgård (61°22'N, 17°02'E), 1990 Nordin 2659 (UPS); Uppland: Harg par., Fagerön, (60°12'N, 18°28'E), 1992 Nordin 3020 (UPS); Jämtland: Rätan par., Vitvattnet (62°21'N, 14°36'E), 2004 Wedin 7583; Ångermanland: Bjurholm par., Nordansjö, Lake Bjärten (63°50'N, 18°59'E), Wedin 29.VI.2004; Västerbotten: Umeå, Tjälamark (63°52'N, 20°12'E), 2003 Wedin 7301, 7302; as above, 2004 Wedin 7604, 7608; Lycksele Lappmark: Lycksele par., Gammplatsen (64°35'N, 18°41'E), 2005 Gilenstam 2670, 2698; Lule Lappmark: Jokkmokk par., Mt. Tapmokerget, (66°21'N, 20°42'E), 1990 Moberg 9235 (UPS); Parkijaur kraftstation (66°45'N, 19°15'E), 2003 Gilenstam 2610, 2618.

Stictis radiata Pers., Obs. Mycol. 2: 73 (1799).

(Figs 2I, 6D–F)

Type: Germany: in cortice pini abietis (L-Persoon 910.63–968–lectotype designated by Sherwood 1977a: 236, not seen).

A widely distributed saprotroph (Fig 2I), which, in our area, has been collected on wood of *Picea abies*, *Populus tremula*, and *Salix caprea*. Further south in Scandinavia it is common on various substrates, particularly wood of *Ulmus*. Ascomata ca 0.3–0.7 mm in diam. Margin white, pruinose, entirely encrusted in crystals, ca 80–100 μ m in cross section, four-layered with (1) an outermost layer including remnants of host

tissue, (2) a proper outer wall layer of hyaline hyphae, (3) a poorly delimited crystalliferous layer where crystals are \pm abundant particularly in the upper part, and (4) a compact and not particularly strongly gelatinized periphysoid layer, formed by branched, interwoven hyphae with a comparatively wide lumen (Fig 6D–F). Disc ochraceous, smooth, glossy, non-pruinose. Hymenium I+ bluish, ca 175–200 μm high; subhymenium ca 20–30 μm thick. Paraphyses not forming a distinct epithecium; no differentiated marginal paraphyses present. Hypothecium/lower ascoma wall poorly defined and hardly visible. Asci ca 150–180 μm . Spores 8, ca 140–160 \times 2–2.5 μm .

Stictis radiata, the type species of the genus *Stictis*, is similar in habit to *S. brunnescens* in having a glossy, distinctly ochraceous ascoma disc and a white pruinose margin, which distinguish these two species from all other Stictidaceae in the area. *S. radiata* is the only *Stictis* species in the area that does not form any differentiated marginal paraphyses or show any pigmentation in ascoma sections. The absence of pigments in the margin and the compact layer of distinctly branched and interwoven periphysoids, are the most easily observed characteristic distinguishing *S. radiata* from *S. brunnescens*.

Known localities: **Sweden:** Ångermanland: Nordmaling par., 3 km NE Norrfors, Mt. Fälltjärnsberget (63°47'N, 19°03'E), 2003 Wedin 7103; Lule Lappmark: Jokkmokk par., Kvikkjokk, Köpenhamn, (17°50'E, 66°55'N), 2001 Gilenstam 2449a, 2450c.

Additional specimens examined: **Sweden:** Öland: Algotsrum par., Lilla Hult. (56°41'N, 16°32'E), 2001 Wedin 6493.

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