The Sticta fuliginosa group in Norway and Sweden

STEFAN EKMAN, TOR TØNSBERG, and PER MAGNUS JØRGENSEN

Ekman, S., Tønsberg, T. & Jørgensen, P. M. 2019. The *Sticta fuliginosa* group in Norway and Sweden. *Graphis Scripta* **31** (4): 23–33. Oslo. ISSN 2002-4495.

A recent investigation demonstrated that *Sticta fuliginosa* (Hoffm.) Ach., as currently treated, includes four distinct species in Europe: *Sticta fuliginosa* s. str., *S. fuliginoides* Magain & Sérus., *S. ciliata* Tayl., and *S. atlantica* Magain & Sérus. This finding prompted us to revise material named *S. fuliginosa* from Norway and Sweden. It is demonstrated here that three species occur in Norway: *S. fuliginosa* s. str., *S. fuliginoides*, and *S. ciliata*. *S. fuliginoides* is the most widespread species, whereas *S. fuliginosa* occurs mostly along the coast and *S. ciliata* is very rare in the most oceanic parts of the western coast. In Sweden, only a single species of the group occurs, viz. *S. fuliginoides*. It was formerly found in scattered sites across the southern half of Sweden but has now disappeared from most of them. The basionym *Sticta fuliginosa* var. *propagulifera* Vain. ex H. Magn. is lectotypified and synonymized under *S. fuliginoides*.

Stefan Ekman, Museum of Evolution, Uppsala University, Norbyvägen 16, SE-75236 Uppsala, Sweden. Email: stefan.ekman@em.uu.se (corresponding author)

Tor Tønsberg, Department of Natural History, University Museum, University of Bergen, Allégaten 41, P.O. Box 7800, NO-5020 Bergen, Norway. E-mail: tor.tonsberg@uib.no

Per Magnus Jørgensen, Department of Natural History, University Museum, University of Bergen, Allégaten 41, P.O. Box 7800, NO-5020 Bergen, Norway. E-mail: pmjorg@broadpark.no

Introduction

The genus *Sticta* is primarily represented in humid mountain forests of the tropics (Moncada & Lücking 2012). The currently accepted number of species is close to 150 but may turn out to be as high as 500 (Moncada et al. 2014). The European members of the genus have essentially remained the same since the monograph by Delise (1825), who listed *S. sylvatica* (Huds.) Ach., *S. fuliginosa* (Hoffm.) Ach., *S. limbata* (Sm.) Ach., and *S. dufourii* Delise. It was later discovered that *S. dufourii* constitutes the cyanobacterial morph of the green-algal *S. canariensis* (Flörke) Delise and was consequently synonymized under the latter, older name (Armaleo & Clerc 1991). Although the number of misidentifications has been substantial and some authors have even expressed doubts about the distinction between *S. sylvatica* and *S. fuliginosa*, they have generally been considered as two relatively easily identifiable species (Degelius 1935).

The status quo of four easily distinguished European species of *Sticta* was drastically shifted with the detailed investigation by Magain & Sérusiaux (2015), which was based on DNA sequence data as well as morphology. The authors convincingly showed that the traditional European circumscription of *S. fuliginosa* actually includes four distinct species: *S. fuliginosa* (Hoffm.) Ach. s. str., *S. fuliginoides* Magain & Sérus., *S. ciliata* Tayl., and *S. atlantica* Magain & Sérus. With the exception of *S. fuliginoides* and *S. ciliata*, these species are probably not even each other's closest relatives. The four species of *S. fuliginosa* were shown to differ morphologically by a combination of growth habit, structure of upper thallus surface, build of the upper cortex, as well as presence or

Copyright Stefan Ekman et al. This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. Published 2019-06-25 by The Nordic Lichen Society, http://nhm2.uio.no/lichens/NLS.

absence of papillae on the cyphella surface cells. The importance of the latter character for distinguishing between species of *Sticta* was first recognized by Moncada et al. (2014).

Although a major breakthrough in our understanding of European *Sticta*, the investigation by Magain & Sérusiaux (2015) was limited to samples from eastern and western France, southwestern England, and southwestern Ireland. Sanderson (2016) later provided an overview of *Sticta* in Britain, in which he built on the morphological findings of Magain & Sérusiaux (2015), clarified characters for separating the species in the field, and concluded that all species of the *S. fuliginosa* complex except *S. atlantica* occur in Britain. Northern European material has so far not been investigated, except for the report of *S. ciliata* from western Norway (Gaarder & Jordal 2016). The aim of this paper is to partially rectify this shortcoming by revising material from Norway and Sweden identified as *S. fuliginosa*.

Material and Methods

All Swedish specimens filed as *Sticta fuliginosa* in LD, GB, S, and UPS, all Norwegian specimens in BG, and a substantial subset of the Norwegian specimens in O, TRH, and UPS were checked. Specimens were examined for macroscopic characters and, when necessary, microscopic characters (papillae on cyphella surface cells, upper cortex). Cyphella surface papillae were studied in hand-made sections mounted in water at 400× or 630× magnification. These papillae are less than 2 μ m long and not clearly visible by inspecting the surface at common magnifications (40–50×) under a dissecting microscope (although the surface cells themselves may appear as inconspicuous 'bumps').

Results and discussions

Three species of the *Sticta fuliginosa* group occur in Norway, namely *S. ciliata*, *S. fuliginoides*, and *S. fuliginosa* s. str. but only *S. fuliginoides* occurs in Sweden. No evidence was found of any additional species not treated by Magain & Sérusiaux (2015) being present in Norway or Sweden. Key morphological characteristics, habitat requirements, as well as the distributions of *S. fuliginosa* s. str., *S. fuliginoides*, and *S. ciliata* in Norway and Sweden are discussed below under the species treatments.

In Sweden, "*Sticta fuliginosa*" is classified as Critically Endangered (CR) on the red-list (ArtDatabanken 2015) and is nationally protected against collecting or any other kind of damage ("Artskyddsförordningen", Swedish Code of Statutes 2007: 845 with amendments). The law as well as the red-list need to be urgently amended to accommodate the fact that all known Swedish records of "*S. fuliginosa*" refer to *S. fuliginoides*.

Key and species treatments

A key to all Nordic species of *Sticta* is provided below. This is essentially an updated version of the keys prepared by Dahl & Krog (1973), Krog et al. (1980, 1994), and Jørgensen & Tønsberg (2007). Subsequently, the three members of the *Sticta fuliginosa* group present in Sweden and Norway are treated. Morphological descriptions were primarily compiled from Magain & Sérusiaux (2015) and Sanderson (2016), although microscopic characters, with the exception of the upper cortex of *S. ciliata*, are based on our observations. The distributional and ecological information pertaining to Norway and Sweden is new.

Key

1	Thallus with marginal (or sometimes also laminal) bluish grey soralia
2.	Thallus bluish grey to grey-brown; lobe margins and upper side densely set with laciniate lobules; rarely producing green-algal lobes with a smooth margin \dots <i>S. canariensis</i> Thallus \pm dark brown; without laciniate lobules; never with green-algal lobes \dots 3
3.	Thallus lobes strap-shaped, dichotomously branched, upper surface shiny when dry, lower surface black (at least near the base); cyphella surface cells without papillae (although cells sometimes budding); upper cortex of $4-5$ cell layers, the uppermost of which is composed of smaller cells than the layers below
	surface \pm brown; never with the combination of smooth cyphella surface cells and an upper cortex with the uppermost cell layer different from the layers below
4.	Young thallus lobes \pm upright and trumpet-shaped with recurved margin, without or with few whitish hairs ('cilia'); upper cortex composed of 4–5 cell layers, the uppermost of which consists of smaller cells than the layers below; cyphella surface cells with 2–6 papillae per cell
_	Young thallus lobes auriculate, flattened, not trumpet-shaped, margin recurved or not; upper cortex composed of 1–3 layers of \pm equally sized cells; cyphella surface cells without or with \geq 15 papillae
5.	Thallus large, without or with a few stiff, whitish hairs ('cilia') on secondary lobes; apothecia rare, with few to numerous, short and soft, whitish or tan hairs attached to the outer side of apothecial margin; cyphella surface cells without papillae
_	Thallus small to medium-sized with abundant stiff, whitish hairs ('cilia') on lobe margins; apothecia frequent, with cilia attached to the upper edge of apothecial margin; cyphella surface cells with 15–20 papillae per cell

Sticta ciliata Taylor

Illustrations: Fig. 1A, 3I-J. Gerault (2019).

Morphology: Sticta ciliata forms small to medium-sized thalli composed of more or less auriculate lobes with a recurved margin in mature thalli (more or less flat in young ones). Apothecia occur frequently, the margin of which is equipped with a characteristic 'crown' of stiff, whitish hairs commonly referred to as 'cilia'. Cyphella surface cells bear abundant papillae, often 15–20 per cell (the number apparently underestimated by Magain & Sérusiaux 2015). The upper cortex is thin, 20–25 µm thick, and consists of 1–3 layers of more or less equally shaped cells (according to Magain & Sérusiaux 2015).

Ecology: This species is known from shaded and moist, more or less north-facing rock walls and once from a trunk of *Salix caprea*. It seems to be dependent on constant and high humidity.

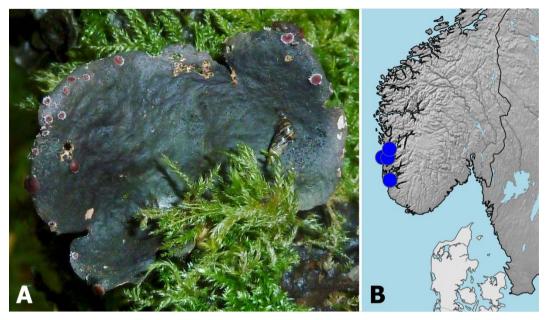


Figure 1. A. Habit of moist *Sticta ciliata* in the field at Prestkonevatnet, Tysnes municipality, Hordaland, Norway. Photo: Geir Gaarder 2012. B. Distribution of *S. ciliata* in Norway.

Distribution: Fig. 1B. *Sticta ciliata* appears to be rare and we have studied material only from a few sites in Rogaland and Hordaland in westernmost Norway. An additional report from Rogaland (Blindheim 2019) has not been checked by us. It can be considered 'extremely oceanic' in the sense of Jørgensen (1996), with a distribution similar to that of, e.g., *S. canariensis*.

Notes: Sticta ciliata can be confused with *S. fuliginoides*; see that species for a comparison. The two species share the modest thallus size, recurved lobe margins, and frequently also the presence of hairs along the edges of young lobes (although normally much fewer in *S. fuliginoides* than in *S. ciliata*). *S. ciliata* can also be confused with *S. fuliginosa*, particularly when the latter is fertile. Marginal hairs are sometimes present in low numbers on secondary lobes of *S. fuliginosa*. Hairs are frequently also present on the apothecial margin, although the hairs, unlike the ones in *S. ciliata*, tend to be shorter, softer and mostly attached to the outer side of the apothecial margin. In addition, *S. fuliginosa* is generally larger, has flat (not recurved) lobe margins, and lack papillae on the cyphella surface cells. Compared to both species, *S. ciliata* is distinguished by the abundance of stiff cilia along the thalline margin (and uppermost edge of apothecial margin when fertile) and the numerous papillae on the cyphella surface cells.

Specimens examined: **Norway**. *Rogaland*: Rennesøy, Dale, in deciduous forest, 1985-12-06, J. I. Johnsen (BG). *Hordaland*: Bømlo, Lykling, along road running parallel with N side of Lyklingfjorden, 2002-06-19, L. Lindblom 1202 (BG L-76761); Bømlo Notland, 2005-10-28, A. Knutsen (BG L-81999); Stord, Bjelland–Gullberg Ø, 2018-04-29, J. T. Klepsland JK18-060 (BG L-102206); Tysnes, praedium Sunde prope Luksund, 1910-08-26, J. J. Havaas (BG L-53106); Tysnes, Prestkonevatnet (Gaarder & Jordal 2016; accepted here as a confirmed record due to a close-up image of a thallus with apothecia that made identification possible).

Sticta fuliginoides Magain & Sérus.

Illustrations: Fig. 3A–E, 4A. Jørgensen & Tønsberg (2007), as *S. fuliginosa*. Timdal (2019), under Photo Gallery. Sanderson (2017), as *S. fuliginoides*.

Morphology: Sticta fuliginoides is often recognizable by its medium-sized, rounded, more or less upright and trumpet-shaped young lobes with a recurved margin. A modest number of whitish hairs is frequently found near the edge of the youngest lobes. Old thalli without young lobes can sometimes be more problematic to identify by the overall habit. However, the species is readily identified by the presence of papillae on the cyphella surface cells. The papillae are modest in number, usually 2–6 per surface cell, and are sometimes branched. The upper cortex is 25–40 μ m thick, and stratified, i.e., composed of 4–5 cell layers, the uppermost of which is made up of thick-walled rectangular cells that are distinctly smaller than the ones below. The upper cortex is sometimes partially abraded in bad specimens, but is usually visible in at least some parts.

Ecology: Sticta fuliginoides is found in more or less humid places, often inhabiting shaded, mossy rocks and occasionally mossy trunks, predominantly of *Salix caprea* and *Sorbus aucuparia* but also, e.g., *Populus tremula, Fraxinus excelsior, Juniperus communis*, and *Picea abies*.

Distribution: Fig. 2A. This species is by far the most widespread member of the *S. fuliginosa* complex in Norway and Sweden. It occurs along the coast from Vest-Agder to the southern parts of Nordland. It reaches east into the inner fjord regions, river valleys, and forested hill areas of central and eastern South Norway and southern Sweden, i.e. areas with an annual precipitation of 500–600 mm. This is much less than what is apparently required by *S. ciliata* and *S. fuliginosa* s. str. Although historically reported from numerous localities in Sweden, it is now extinct from most of them. Sites where it is still present (green dots in Fig. 2A) are found in Östergötland, Dalsland, Värmland, and Dalarna. In the Norwegian material, specimens from Vest-Agder, Telemark, Buskerud, Hedmark, Rogaland, Hordaland, Sogn og Fjordane, Møre og Romsdal, Sør-Trøndelag, Nord-Trøndelag, and Nordland were studied.

Notes: For a comparison with *S. fuliginosa*, see under that species. Specimens of *S. fuliginoides* with hairs on young lobes can be mistaken for *S. ciliata*. That species, however, differs from *S. fuliginoides* by the distinctly larger number of papillae on the cyphella surface cells, generally smaller thallus size, the lack of trumpet-shaped young lobes, and the abundance of hairs ('cilia') on the upper side of the lobe edges.

Taxonomy and nomenclature: The name Sticta fuliginosa f. propagulifera Vain. ex H. Magn. (Magnusson 1929) has been used for specimens with isidia developing into 1-2(-3) mm wide lobules. The name was based on material collected by Johan Havaas in Hole municipality in Buskerud, southeastern Norway, from where the same morph was collected between 1905 and 1968. The type material of this name agrees well with *S. fuliginoides* in all other respects (growth habit, papillae on cyphella surface cells, upper cortex). *S. fuliginosa* f. propagulifera is consequently reduced here into synonymy with *S. fuliginoides* (see lectotypification below).

Lectotypification: Stictina fuliginosa f. *propagulifera* Vain. in Havaas, Lich. exs. Norveg. 275 (1905), nomen nudum. – *Sticta fuliginosa* f. *propagulifera* Vain. ex H. Magn., Flora över Skandinaviens busk- och bladlavar: 35 (1929). Type: Norway, Buskerud, Hole municipality, "Krokkleven på Ringerike", 1905-07-17, J. J. Havaas in Havaas: Lich. exs. Norveg. 275 (UPS L-136824, lectotype, designated here, seen by PMJ and SE; MBT386016).

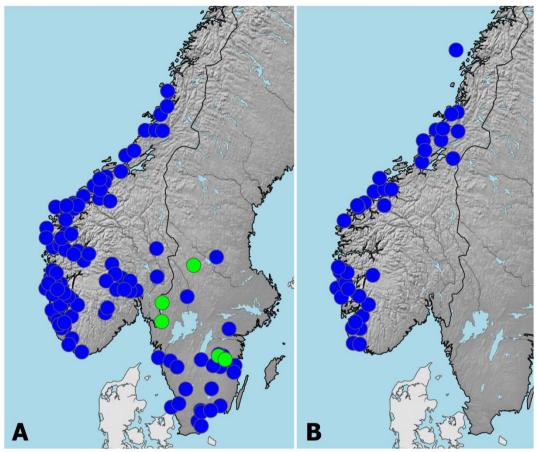


Figure 2. Distributions of *Sticta* species in Norway and Sweden. A. *S. fuliginoides*. Green dots in Sweden refer to contemporary localities. B. *S. fuliginosa*.

Specimens examined: Norway. Only a selection of specimens is listed here, viz, one per province. Hedmark: Nord-Odal, Ekornhol, Klomma, 2004-09-29, J. T. Klepsland L-40 (O L-133854). Buskerud: Hole, Krokkleven, 1926-09, B. Lynge (O L-13828). Telemark: Seljord, Hønsegjuvet river gorge, W of Vårbulii, 1991-05-02, R. Haugan, K. Isaksen & H. Rinden H2017 (O L-12161). Vest-Agder: Lyngdal, Lyngdalsfjorden, near Sjunderaasen, 1953-06-23, R. Santesson (UPS L-133433), Rogaland: Sokndal, Seljuåsen ved Rægefjord, 1905-08-06, J. J. Havaas (BG L-53060). Hordaland: Vaksdal, the E-facing hillside W of Bolstadfjorden, just W of the road from Dalseid to Stamnes, SW of the S mouth of the tunnel just N of Geitabottsberget, 2006-09-07, T. Tønsberg 37298 (BG L-83164). Sogn og Fjordane: Leikanger, Hermansverk, Hjellane, 1991-05-09, G. Gaarder 430 (BG L-12840). Møre og Romsdal: Tingvoll, Skjellberget, 1996-04-14, G. Gaarder 1743 (BG L-32591). Sør-Trøndelag: Åfjord, E-facing slope N of lakes Austdalsvatna, 1995-08-29, H. Holien 6846 (TRH L-3353). Nord-Trøndelag: Nærøy, Foldereid, the ravine E of Bergshatten, 1980-07-06, T. Tønsberg 4950 (BG L-53122). Nordland: Brønnøy, NE-facing slope of Liaheia, 1992-06-02, H. Holien 5083 (TRH L-1523). Sweden. All records listed as S. fuliginosa by Degelius (1935) are included here, except the specimens from Skåne, Västra Vram, 1891, G. O. Malme, and Småland, Femsjö, 1851, T. M. Fries, which were overlooked in herb. S because they are filed under S. sylvatica. Skåne: Brunnby par., Kullen, ovan Svartehäll (Kullens nordsida), 1934-08-05, R. Santesson (S F158253, UPS L-112250, UPS L-163905); Käringamalen, Kullen, 1934-08-05, Y. Thulin (UPS L-131069); Kullaberg, ovan Käringamalen, 1935-06-29, G. Degelius (UPS L-

112251). Degeberga par., Forsakar, 1890-06, G. O. Malme (UPS L-002161), Forsakar, 1890-06-03, G. O. Malme (LD 1087594, S F158248), Forsakar, 1891-06-16, G. O. Malme (S F158250). Hjärsås par., Vrångefälle, 1932-06-01, C. Stenholm (GB 0159198, S F158251, UPS L-002160, UPS L-157134). Oppmanna par., Boknäset, 1890, G. O. Malme (S F158249), Södra Mellby par., Stenhuvud, 1900-06-30, B. Nilsson-Kajanus (S L14779). Blekinge: Karlshamn par., Karlshamn, 1871, J. Hulting (GB 0159201, LD 1007119, S F158252); Karlshamn, 1871-07, J. Hulting (UPS L-002162). Tving par., 1873, H. Falk (LD 1087530, S F158259, UPS L-002163); Alnaryd, 1873-08, H. Falk (S F158254, UPS L-163904). Småland: Eksjö par., Eksjö stad, Prästängen, nära sjön Hunsnäsen, 1910-03-12, P. Johansson (S F158261); Prästängen, vid Hunsnässjön, 1910-03-12, P. Johansson (S F158262, UPS L-112254), Femsjö par., Hägnaklippan, probably in the 1820s, E. Fries in Fries: Lich. Suec. exs. 79 (UPS L-939817, mixed in specimen of S. sylvatica); 1859, O. G. Blomberg (S F158255); Hägnen, 1926-08-18, G. Degelius (UPS L-112258), Gårdsby par., branten S om Stensjön ("Gripenberg"), 1937-11-07, B. Hedvall (LD 1087338); vid Stensjön, 1940-10-02, B. Hedvall (LD 1087210, UPS L-002176). Hjorted par., S om Norrhult, i sluttningen mot ån, 1938-09-06, T. E. Hasselrot (S F158260). Ingatorp par., Ingatorp, 1888-10, R. Tolf (GB 0159199, LD 1087466, S F158256, S F258257, S F158258, UPS L-002164, UPS L-157135). Kristdala par., Mjölkulle, 1935-01-30, E. Evers (S F158264). Skärstad par., Vistakulle, 1929-07-03, B. Hedvall (LD 1006991, UPS L-112253); Vistakulle, 1934-08-19, B. Hedvall (LD 1087402, S F158263, UPS L-112256). Halland: Östra Karup par., på Åsen, 1866, F. Elmqvist (LD 1071200, mixed in specimen of S. sylvatica). Bohuslän: Lycke par., Älgön, N-sidan, 1965-05-30, G. Degelius & S. Wall (UPS L-112260). Dalsland: Nössemark par., 1992-06-13, C. Kannesten (photos seen by SE). Västergötland: Viskafors par., Svaneholm, 1918-06, C. Sandberg (LD 1087018). Skallsjö par., Näs slott, vid stranden av Sävelången, 1959-07-24, T. E. Hasselrot (S F158265). Östergötland: Horn par., 2000-10-12, M. Hagström (also seen in the field 2017 by SE together with MH). Malexander par., 2015-06-19, M. Hagström (photos seen by SE); Högbo, nära landsvägen, 1935-08-15, T. E. Hasselrot (S F158267, UPS L-002168, UPS L-157136); mellan Högbo och Svärdsvik, 1937-11-02, G. Degelius & T. E. Hasselrot (UPS L-112257). Skedevi par., Rejmyre, undated, H. von Post (UPS L-002165); Rejmyre, 1852, H. von Post (S F158266). Kisa par., vid vägen till Tomestorp, 1935-08-13, T. E. Hasselrot (S F158268, S F158269, UPS L-112255). Värmland: Munkfors par., Ö om Skalltjärn, 1962-06-30, S. Sundell 2676 (UPS L-009418, UPS L-157137). Östervallskog par., 1988-08-02, C. Kannesten (photos seen by SE). Dalarna: Boda par., Styggforsen, 1940-06-18 (UPS L-112261), Styggforsen, 1940-06-20, H. Persson (UPS L-002167); Styggforsen, 1946-07-25, T. E. Hasselrot (GB 0159200, LD 1086890, S F158270). Malung par., 2008-05-04, J. Hermansson (UPS L-564790).

Sticta fuliginosa (Hoffm.) Ach. s. str.

Illustrations: Fig. 3F-G, 4B. Gerault (2019) as "Sticta fuliginosa ss. str.".

Morphology: Sticta fuliginosa can be recognized by the large, irregularly auriculate thalli without marginal cilia and with a flat (as opposed to recurved) margin. Sections through the thallus reveal the cyphella surface cells, which are smooth (lack papillae) and come across as an extension of the outermost cell layer of the lower cortex. The upper cortex is thin, $12-20(-23) \mu m$ thick, and composed of 2–3 layers of more or less equally shaped cells (the uppermost cells not distinctly smaller than the ones below). Apothecia seem to be rare, when present with few to many, whitish to tan, short and soft hairs attached to the outer side of apothecial margin.

Ecology: Sticta fuliginosa seems to prefer old deciduous trees, e.g. *Fraxinus excelsior* and *Sorbus aucuparia*, or wet, mossy rock-faces in gradually more humid localities to the north. In the rainforests of Nord-Trøndelag and Nordland, it also inhabits thin branches of *Picea abies*.

Distribution: Fig. 2B. This species is rare and known from scattered localities along the coast of Norway in the counties Rogaland, Hordaland, Sogn og Fjordane, Møre og Romsdal, Sør-Trøndelag, Nord-Trøndelag, and Nordland.

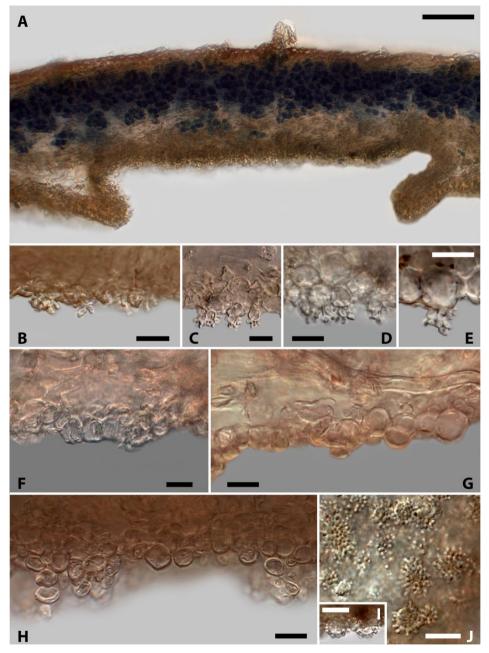


Figure 3. Sections through cyphellae in *Sticta*. A–E. *S. fuliginoides*, showing section through entire cyphella (A) and cyphella surface cells with papillae (B–E). F–G. *S. fuliginosa*, cyphella surface cells without papillae. H. *S. sylvatica*, cyphella surface cells with a tendency to bud new cells but without papillae. I–J. *S. ciliata*, cyphella surface cells with papillae. Scales: 0.1 mm (A), 10 µm (B–J). Photos of UPS L-112257 (A), L-157135 (B), L-002176 (C–E), L-112259 (F), L-157159 (G), L-112252 (H), and L-834342 (I–J).

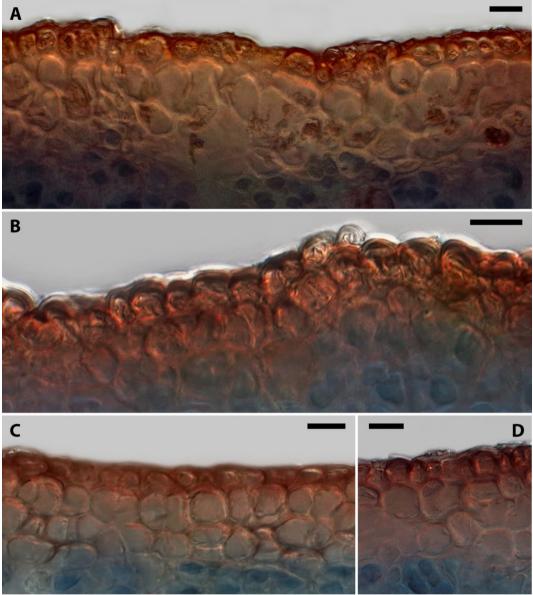


Figure 4. Sections through upper cortex in *Sticta*. **A**. *S. fuliginoides*. **B**. *S. fuliginosa*. **C–D**. *S. sylvatica*. Scales: 10 μm (A–D). Photos of UPS L-133433 (A), L-157159 (B), GB 0159196 (C), and UPS L-157187 (D).

Notes: Sticta fuliginosa can be confused with old and large specimens of *S. fuliginoides* that sometimes lack the characteristically trumpet-shaped lobes. In such cases, *S. fuliginoides* can be separated by the presence of papillae on the cyphella surface cells, and the thicker and stratified upper cortex. *S. fuliginosa* and *S. sylvatica* share the lack of papillae on the cyphella surface cells (Fig. 3H). *S. sylvatica* is normally easily recognized by its strap-shaped and dichotomously

branched thallus, black lower side, and shiny upper surface. Poorly developed herbarium specimens, however, can be difficult to identify, in which case *S. fuliginosa* and *S. sylvatica* can be distinguished by their different upper cortex, thin and unstratified in the former (Fig. 4B), thick and stratified in the latter (Fig. 4C–D). In addition, the cyphella surface cells in *S. sylvatica* are distinctly different in shape and size from the outermost cell of the lower cortex, forming an uneven, irregular surface of globose to ellipsoid cells that tend to bud (Fig. 3H). When fertile, *S. fuliginosa* might be mistaken for *S. ciliata* when hairs are present on the apothecial margin. Hairs ('cilia') on the apothecial margin of *S. fuliginosa* are shorter and softer than in *S. ciliata*, and are attached to the outer side of the apothecial margin, not the upper part of the edge as in *S. ciliata*.

Specimens examined: Norway. Only a selection of specimens is listed here, viz. one per province. Rogaland: Sandnes, Høle, i lien ovenfor Trodal, 1967-03-22, P.M. Jørgensen (BG L-53069). Hordaland: Austevoll, Selbjørn, Gaukstein, 2003-05-21, T. Tønsberg 31819 (BG L-76060). Sogn og Fjordane: Lærdal, Råsdalen, 2002-07-27, G. Gaarder 4035 (BG L-75510). Møre og Romsdal: Ålesund, Høgnakken, 1998-10-25, D. Holtan (BG L-48580). Sør-Trøndelag: Roan, the highest point along the road between Hellefjorden and Berkelandsfjorden, 1980-07-07, T. Tønsberg 4964 (BG L-53124). Nord-Trøndelag: Flatanger, Stordalen, 1995-06-12, H. Holien 6505 (TRH L-2566). Nordland: Træna, Sanna, 2007-07-14, G. Gaarder 4783 (TRH L12810).

The remaining European species

Amongst the three remaining species previously known from Norway and Sweden, Sticta canariensis (Flörke) Delise is the rarest, displaying an 'extremely oceanic' distribution in western Norway (Jørgensen 1996) and being red-listed as vulnerable (VU) in Norway (Timdal et al. 2015). This species was first reported from Norway by Jørgensen (1970). Only the cyanobacterial morph of this species is known to occur in a free-living state in Norway, although composite thalli, with a few small green-algal lobes on otherwise cyanobacterial individuals, have been observed infrequently (Tønsberg 1990, Jørgensen & Tønsberg 2007, Fadnes & Knutsen 2014). S. limbata (Sm.) Ach, is widespread along the entire western coast of Norway (Degelius 1935) but considered regionally extinct (RE) in Sweden (ArtDatabanken 2015). It was previously known from a few sites in southwestern Sweden and has not been recorded there since 1986 (Hultengren 2005). S. sylvatica (Huds.) Ach. is widespread in southern Norway along the coast and in the ford regions north to Sogn og Fjordane. It is rare in southeastern Norway, with a few, both old and recent, records in inland valleys in Aust-Agder, Buskerud and Telemark, as well as a single old (1868) record from the Oslofjord area. In Sweden, S. sylvatica is red-listed as critically endangered (CR) (ArtDatabanken 2015). Historically, it has been recorded from scattered sites in southern Sweden (Degelius 1935), but is currently known only from a few places in Småland, Östergötland, and possibly Värmland (Hultengren 2005). This is the only one of the species discussed here that could potentially be confused with members of the S. fuliginosa group, particularly S. fuliginosa s. str. (see under that species for the morphological distinction).

The fourth European species of the *S. fuliginosa* group, *S. atlantica* Magain & Sérus., is recognized by the presence of irregular swellings on the upper surface, on which isidia start their development. It has so far been reported from a few sites in the Azores and southwestern Ireland (Magain & Sérusiaux 2015). We have not come across any candidate specimens for this species in the Norwegian and Swedish material.

Dedication: This paper is dedicated to Roland Moberg on the occasion of his 80th birthday.

Acknowledgements: Geir Gaarder kindly put the photograph of *Sticta ciliata* at our disposal. Mikael Hagström and Claes Kannesten provided images from contemporary Swedish localities, and Mikael provided invaluable guidance during fieldwork in Östergötland. We are also indebted to the curators of the cited herbaria for loans and assistance.

References

- Armaleo, D. & Clerc, P. 1991. Lichen chimeras: DNA analysis suggests that one fungus forms two morphotypes. *Experimental Mycology* 15: 1–10.
- ArtDatabanken 2015. Rödlistade arter i Sverige 2015. ArtDatabanken SLU, Uppsala, 209 pp.
- Blindheim, T. 2019. BioFokus. Version 1.1057. BioFokus. Occurrence dataset https://doi.org/10.15468/jxbhqx. URL: https://www.gbif.org. [Accessed 3 June 2019.]
- Dahl, E. & Krog, H. 1973. Macrolichens of Denmark, Finland, Norway, and Sweden. Universitetsforlaget, Oslo, 185 pp.
- Degelius, G. 1935. Das ozeanische Element der Laub- und Strauchflechtenflora von Scandinavien. Acta Phytogeographica Suecica 7: 1–411.
- Delise, D. 1825. Histoire des lichens. Genre Sticta. Mémoires de la Société linnéenne du Calvados 1825: 3– 167.
- Fadnes, P. & Knutsen, A. 2014. Stort mangfold av sjeldne og rødlistede karplanter, oseaniske lav og moser og beitemarksopp i kulturlandskapet på Spyssøya, Bømlo, Hordaland. *Blyttia* **72**: 100–114.
- Gaarder, G. & Jordal, J. B. 2016. Fattig boreonemoral regnskog og andre naturtyper påvist i Hordaland 2014–2015. *Miljøfaglig Utredning Rapport* **2016-03**: 1–35.
- Gerault, A. 2019. *Lichen marins, maritimes et océaniques*. URL: http://www.lichensmaritimes.org. [Accessed 29 May 2019.]
- Hultengren, S. 2005. Åtgärdsprogram för bevarande av ärrlavar. Naturvårdsverket Rapport 5470: 1-38.
- Jørgensen, P. M. 1970. Sticta dufourii Del. and its parasymbiont Arthonia abelonae P.M. Jørg. n. sp. in Norway. Nova Hedwigia 18: 331–340.
- Jørgensen, P. M. 1996. The oceanic element in the Scandinavian lichen flora revisited. *Symbolae Botanicae* Upsalienses **31**: 297–317.
- Jørgensen, P. M. & Tønsberg, T. 2007. Sticta. In: Ahti, T., Jørgensen, P. M., Kristinsson, H., Moberg, R. Søchting, U. & Thor, G. (eds), Nordic Lichen Flora, Volume 3. Nordic Lichen Society, Uppsala, pp. 84–86.
- Krog, H., Østhagen, H. & Tønsberg, T. 1980. Lavflora. Norske busk- og bladlav. 1st ed. Universitetsforlaget, Oslo, 312 pp.
- Krog, H., Østhagen, H. & Tønsberg, T. 1994. Lavflora. Norske busk- og bladlav. 2nd ed. Universitetsforlaget, Oslo, 368 pp.
- Magain, N. & Sérusiaux, E. 2015. Dismantling the treasured flagship lichen *Sticta fuliginosa* (Peltigerales) into four species in Western Europe. *Mycological Progress* 14: 1–33.
- Magnusson, A. H. 1929. Flora över Skandinaviens busk- och bladlavar. Nordstedt & Söner, Stockholm, 127 pp.
- Moncada, B. & Lücking, R. 2012. Ten new species of *Sticta* and counting: Colombia as a hot spot for unrecognized diversification in a conspicuous macrolichen genus. *Phytotaxa* 74: 1–29.
- Moncada, B., Lücking, R. & Suárez, A. 2014. Molecular phylogeny of the genus Sticta (lichenized Ascomycota: Lobariaceae) in Colombia. Fungal Diversity 64: 205–231.
- Sanderson, N. A. 2016. The field identification of the species within *Sticta fuliginosa* s. lat. in Britain. *British Lichen Society Bulletin* **119**: 2–14.
- Sanderson, N. A. 2017. Wessex lichen group. URL: http://wessexlichengroup.org. [Accessed 29 May 2019.]
- Timdal, E. 2019. *The Lichen Herbarium*. URL: http://nhm2.uio.no/lav/web. Natural History Museum, University of Oslo. [Accessed 29 May 2019.]
- Timdal, E., Bratli, H., Haugan, H., Holien, H. & Tønsberg, T. 2015. Lav. 'Lichenes'. In: Henriksen, S. & Hilmo, O. (eds). *Norsk rødliste for arter 2015*. Artsdatabanken, Norge.
- Tønsberg, T. 1990. The green algal phototype of Sticta canariensis found in Norway. Graphis Scripta 3: 27.