Ecology and phenology of Illosporiopsis christiansenii

Background

October 2023 marked the centenary of the first record of Hobsonia christiansenii in Germany:

"near Flensburg, along a road at the *Marienhölzung* woods, on *Physcia tenella* on *Ulmus* sp., 4 October 1923, C.F.E. Erichsen, herb. Christiansen 594"

However, this lichenicolous (lichen inhabiting) fungus (LF) was not reported in the UK until 1985 (Lowen *et al.*,1986). *H. christiansenii* was subsequently renamed *Illosporiopsis christiansenii* (B.L. Brady & D. Hawksw.) D. Hawksw. because it was considered more closely related to *Illosporium carneum* (Sikaroodi *et al.*, 2001).

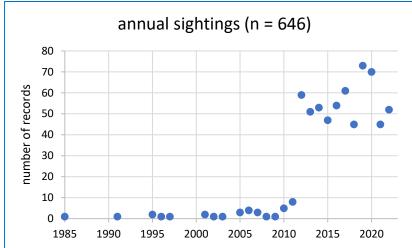
The earliest British Lichen Society (BLS) record is by Steve Chambers in 1991. Recording of *Ill. christiansenii* shot up dramatically in 2012 to an average 55 sightings per year. Its distribution has been mapped across the UK and Ireland and it is classed as Nationally Scarce but of Least Concern (Fig. 1).

Figure 1 *Illosporiopsis christiansenii* with *Physcia tenella* and *Xanthoria parietina*, UK sightings and distribution in the UK and Ireland (up to the end of 2022)

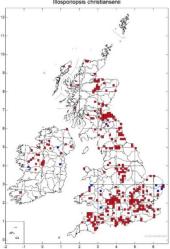
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Sightings: BLS database, LCIG reports, Lowen *et al* (1986) n= total sample size

Map: BLS database







Surprisingly little is known about *Ill. christiansenii* apart from the shocking-pink cirrhi it produces in the autumn and winter months. These are mucus-bound, helically coiled masses of conidia (Lowen *et al.*, 1986) and appear to be the only method of propagation; a sexual form is not known. Hydration causes a reversible swelling of the cirrhi (Claypole *et al.*, 2023) which is believed to play a role in conidial dispersal. Initial wetting of many mucilaginous fungal spores causes the mucilage to swell, leaving the spores suspended in a thin film of water from which they can be dispersed, for example, by splash (Gregory *et al.*, 1959).

A century on, these studies of *Ill. christiansenii* aimed to shed light on its host lichen, substrate and phenology, and its relationship with the host lichen.

Resources and methodology

Fieldwork *Ill. christiansenii* was observed and monitored *in situ* at three UK sites in regions of moderate pollution; all specimens were in an upward-facing, horizontal habit, 1–2 m above ground level (Fig. 2). The sites were monitored throughout 2022 and into spring 2023.

Figure 2 The three field observation sites (left to right): Site 1, VC23, Oxfordshire: healthy lichenised *Malus* branches in an urban garden, Site 2, VC63, South-west Yorkshire: senescent *Fraxinus* twig on a canal towpath, Site 3, VC38, Warwickshire: painted metal gate to a field in a country lane. The arrows point to the position of the LFs observed.



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Site 1. VC23, Oxfordshire, SP531052 with *Physcia adscendens* on healthy, well-lichenised *Malus* tree branches in an urban back garden

Site 2. VC63, South-west Yorkshire, SE063236 with *P. adscendens* on a senescent *Fraxinus* twig on a canal towpath

Site 3. VC38, Warwickshire, SP314546 with *P. tenella* on a painted metal, barred gate to a field alongside a country lane

The field studies were assisted by members of the Zoom Lichen Chat and Improvement Group (LCIG) and the post-LABS group, ABLE. Di Napier monitored Site 3. Steve Chambers contributed data from VC46 (Cardiganshire) and valuable discussion.

Records The BLS database and observations from the LCIG provided 645 records of *Ill. christiansenii*, offering a good overview from 1991 to the end of 2022. BLS records of *P. adscendens*

and *P. tenella* were also consulted. The BLS records provide the raw data for the BLS species distribution maps, but in this study, they were analysed irrespective of geographical location.

Photographs A wide array of material from around the world was accessed via the internet and social media to compare with the photographs taken during this study.

The host lichen

Ill. christiansenii has been reported associated with a number of species in nutrient-rich *Xanthorion* communities, most commonly with *Physcia*, *Physconia* and *Phaeophyscia* species (Lowen *et al.*, 1986). *Xanthoria* species are also reported as host, along with a range of other lichens (Preece, 2011). Nutrient-rich communities usually comprise a number of lichen species. In the field it can be very difficult to determine the host in an often dense, mixed community. However, most LFs tend to be specific to a single species or group of species (Hawksworth, 1982). As many as 95% are thought to be associated with just a single lichen genus (Lawrey & Diederich, 2003). If *Ill. christiansenii* is host specific, which lichen is the most likely primary host?

541 records of *Ill. christiansenii* included the presence of a lichen. Over 82% of these recorded *Physcia*, *Physconia* and *Phaeophyscia* species as host (Fig. 3). Several noted that the *Physcia* thallus was damaged. Only 17% cited *Xanthoria* as sole host. All other lichens represented less than 2% and can be considered as simply growing nearby.

Figure 3 Lichens recorded as associated with *Ill. christiansenii.* 541 records included the presence of one or more possible host lichen; figures in brackets (*) are records with only one possible host lichen (sole host).

associated lichen	numb	er of records
Physcia tenella	290	(264*)
Physcia adscendens	89	(80*)
Physcia aipolia	5	
Physcia dubia	2	
Physcia stellaris	2	
Physcia leptalea	1	
Physcia spp. unspecified	47	
Phaeophyscia orbicularis	3	
Physconia distorta	2	
Xanthoria parietina	119	(92*)
Xanthoria polycarpa	1	
Parmelia spp.	8	
Halecania viridescens	2	
Melanelixia spp.	2	
Caloplaca cerinlla	1	
Candelaria concolor	1	
Candelariella reflexa	1	
Evernia prunastri	1	
Ramalina fastigiata	1	

50 images of *Ill. christiansenii* from a range of sources were examined to assess the host lichen, including several claiming *Xanthoria* as host. Many pictured damaged *Physcia*, in some cases almost completely destroyed. *Xanthoria* was often present. This study did not reveal any photographs where evidence of a nearby *Physcia* species was not detectable.

At all three field observation sites, the irregular bright-pink *Ill. christiansenii* cirrhi arose in areas of damaged *Physcia* thallus. The host thallus was frequently (but not always) close to *X. parietina*.

Conclusion Based on the records, *Xanthoria* cannot be excluded as host lichen to *Ill. christiansenii*. Fieldwork and photographic evidence, however, strongly support an association with *Physcia*, *Physconia* and *Phaeophyscia* species.

P. adscendens and *P. tenella* represented 81% of the named *Physcia* species recorded as host. Between 2011 and 2022, 87 of these were recorded with *P. adscendens* and 276 with *P. tenella*: a ratio of 2:6. For the same period, the total records of *P. adscendens* (4809) and *P. tenella* (7437) give a ratio of only 2:3. This suggests that less than 1.8% of *P. adscendens* was recorded as infected with *Ill. christiansenii*, compared to 3.7% of *P. tenella*.

Between 1985 and 2022, *P. adscendens* records scattered around 400 annual sightings, but *P. tenella* records rose steadily from just 100 in 1985 to roughly 700 in 2022. According to Janet Simkin (Data Manager of the BLS database) this may reflect recorder bias since there are fewer records from urban areas where *P. adscendens* seems to dominate. However, a similar increase was also observed in other European countries and has been attributed to the effects of nitrogen pollution (van Herk, 1999).

Care should be taken when interpreting records. An individual record is only a snapshot taken by the recorder of the presence of a lichen or LF. It may be inaccurate, such as confusion of *Ill. christiansenii* with *Erythricium aurantiacum* or *Marchandiomyces corallinus* (Claypole *et al.*, 2023). A record gives no indication of the size of the population even on a single tree, or of how many trees nearby also carry the same species, or of how many such 'potential' host thalli are infected. Only a single record is submitted.

The substrate

According to the literature, *Ill. christiansenii* is lichenicolous (Lowen *et al.*, 1986), corticolous (Powell, in Dobson, 2018), living on the protococcoid algal crusts or even crustose lichens such as *Scoliciosporum chlorococcum* (Lowen *et al.*, 1986). Closer inspection of infected lichens suggests necrotic host thallus as another possible substrate.

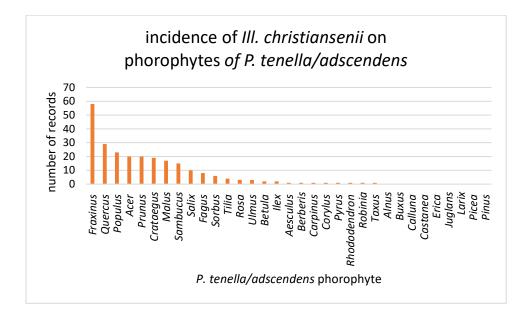
The records were inconclusive and yielded at least two potential substrates. Firstly, most recorders had entered lichenicolous as substrate, but was this observation or prior knowledge of the species? Fourteen had recorded corticolous.

271 records included the substrate of the associated host lichen. 91% were on the bark of 24 deciduous trees (the phorophyte), many noted as "nutrient-rich", with *Fraxinus* leading the field (Fig. 4a). There is a single record of *Ill. christiansenii* with *P. tenella* on a coniferous phorophyte, *Taxus*, in VC22 (Berkshire). In VC46 (Cardiganshire), where *P. adscendens* is not abundant, Chambers (2023) reports *P. tenella* as the primary host on 16 deciduous phorophytes, a single sighting on *Taxus* being the only exception. Twelve of the VC46 phorophytes correspond to phorophyte genera for *P. tenella* and *P. adscendens* in the national records.

Chambers (*ibid*) points out that while *P. tenella* has been recorded on 63 phorophytes in VC46, *Ill. christiansenii* has only been found on roughly a quarter of them, all pronounced nitrophiles. The

same comparison was made using the national records of *P. tenella* and *P. adscendens* from 2011 to 2022. *Ill. christiansenii* has been recorded with these lichen hosts on roughly two thirds of their phorophytes (Fig. 4a).

Figure 4a Substrate of the *Ill. christiansenii* host lichens *P. tenella* and *P. adscendens* (2011 to 2022). Of 271 substrate records, 91% were corticolous on 24 deciduous trees (phorophyte). The lichens associated with bark substrates were 85% *Physcia* spp. and 2% *Xanthoria* spp.



6% of the 271 substrate records were on stone or painted metal, all of which were on *Physcia* species (Fig. 4b). The remaining 3% were on hewn wood. At two of the field sites, the *Physcia* host was on bark and at the third on painted metal.

Figure 4b Substrate of the *Ill. christiansenii* host lichens. 6% of substrate records were on stone or paint. The photographs show *Ill. christiansenii* with *P. tenella* on painted metal below the *Malus* tree at Site 1.

substrate	total records	associated Physcia species	
painted metal	4	P. tenella (3) P. adscendens	
sandstone	5	P. tenella (2) P. dubia (2) P. adscendens	
limestone	2	P. adscendens, Physcia sp.	
granite	2	P. tenella	
drystone walls	1	P. tenella	
concrete	1	P. leptalea	
rocky outcrop	1	P. tribacia	
ironstone	1	<i>Physcia</i> sp.	

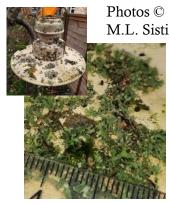
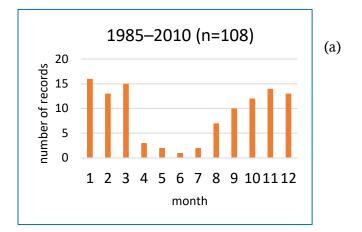
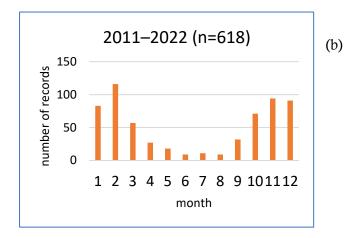
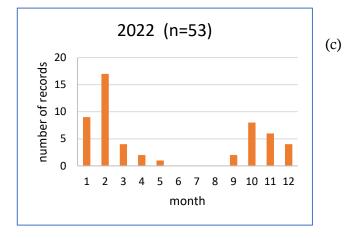


Figure 5 Monthly sightings of *Ill. christiansenii:* (a) 1985–2010 (Preece + BLS records) and (b) 2011–2022 (BLS + LCIG records) compared with (c) the actual timeline of sightings during 2022 (BLS + LCIG records). Total sample size (n) is shown for each case.







Conclusion While most descriptions of *Ill. christiansenii* associate it with nutrient-rich lichen communities on the bark of deciduous trees, this is clearly not the only habitat where it can be found. Since it is associated with *Physcia* species on stone and paint, it cannot be solely corticolous. Rather it is a strong indication that it can either sporulate away from its feeding site or that it can feed on nutrients remaining from unobservable, disintegrated host tissue.

The host lichen and the green slime (necrotic host tissue and algal crust) are both possible substrates. The main association seems to be with *Physcia* and is perhaps linked to its occurrence in habitats with high levels of nitrogen (Pitcairn *et al.*, 2006).

The phenology

The bright pink cirrhi of *Ill. christiansenii* are the only part of the fungus that is observed. Preece (2011) listed the earliest UK sightings and noted that the cirrhi were generally not seen in the summer. He plotted records from 1985 to 2010 against the month of sighting and confirmed this seasonality. These records are not included on the BLS database. The early BLS records fit Preece's phenology, so they were combined to increase sample size. For the period 1985–2010 cirrhi appeared between August and March and there were fewer sightings in the intervening months (Fig. 5a).

There are considerably more records after 2010. If these are plotted in the same way (Fig. 5b), the pattern is similar, but the summer period of low activity is longer, and the highest activity is in February. For VC46 (Cardiganshire), from 1997 to 2023 and a sample size of 99, Chambers (2023) also reports a low activity period in the summer, with peaks in February and November (this data is largely included in the BLS records).

The actual timeline recorded for 2022 is shown in Figure 5c with a clear peak of activity in February and a long period of few sightings from late spring to early autumn. This was observed *in situ* at the three field sites and across the country as reported by the LCIG.

The phenology has clearly changed. To investigate how this had occurred over time, the data from 2011 to 2022 was divided into 4-year blocks, with roughly 200 records in each. Consecutive periods were compared. Two major shifts occurred between 2011 and 2018 which are described in detail in Fig. 6a–c.

To double check that the phenology is not a result of the behaviour of the recorders, the sightings for the primary hosts, *P. tenella* and *P. adscendens*, were also plotted against the month of recording. The result was the inverse of the phenology of the LF (Fig. 6d).

Conclusion The autumn-winter reproductive season of *Ill. christiansenii* in the UK has become shorter by starting later and ending earlier.

Relationship between Ill. christiansenii and the Physcia host

Lichenicolous fungi live on or in lichens, at least at some stage in their life cycle, most commonly as host-specific parasites, but also as broad-spectrum pathogens, saprotrophs or commensals (Lawrey & Diederich, 2003). Lowen *et al.* (1986) considered *Ill. christiansenii* to be "a mild pathogen, sometimes eventually destroying the thalli on which it occurs." It has been suggested that some lichenicolous fungi are weak pathogens, attacking thallus that is already infected or damaged (Powell) and that the relationship may change. Others have been reported to destroy parts of thalli and then persist as a saprobe on the substrate upon which the lichen had been growing e.g., *Refractohilum achromaticum* on *Parmelia sulcata* thalli. It is unclear whether such fungi should be regarded as pathogens, whether they just colonize weakened thalli (weakly parasitic), or whether they are facultative saprobes (Hawksworth, 1982).

Figure 6 Phenology of Ill. christiansenii

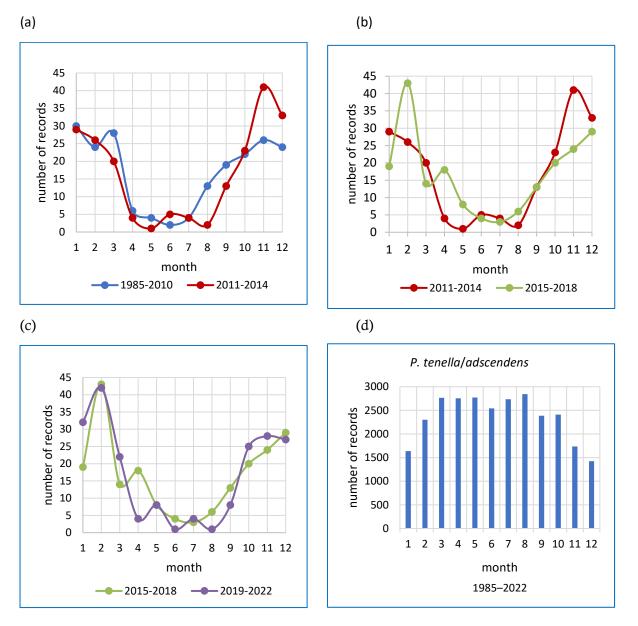
(a) Monthly sightings 1985–2010 compared with 2011–2014. The low activity period lengthened into the autumn through reduced activity in August and September and a corresponding increase in activity in November and December.

(b) Monthly sightings 2011–2014 compared with 2015–2018. The peak of activity shifted from November to February.

(c) Monthly sightings 2015–18 compared with 2019–2022 show no major change.

(All data sets adjusted for a total of 200 records)

(d) Phenology of lichenologists: total monthly records of *Ill. christiansenii* primary hosts, *P. tenella* and *P. adscendens*, as an indication of the monthly activity of the recorders (n=28,308). The phenology is the inverse of that of *Ill. christiansenii*.



Several records indicated that the *Physcia* host thallus appeared dead or unhealthy or that the cirrhi were emerging in thallus debris or on nearby bark. This was confirmed by observations in the field. The cirrhi did not appear to be erumpent from the host thallus as originally described by Lowen *et al.* (1986). They were next to the thallus or at some distance from it.

Progressive damage to the host lichen thallus was observed at all three sites. The infection caused bleaching and browning of the tissue, spreading across the thallus and degrading it. This proceeded irrespective of the presence or absence of cirrhi.

At Site 2, healthy *P. adscendens* on a senescent *Fraxinus* twig was steadily reduced to mere traces in the course of the year and at Site 3 healthy *P. tenella* was severely damaged within six months, along with the *X. parietina* that it was physically supporting (Fig.7).

In the autumn, cirrhi arose in areas where thallus had been destroyed several months before. They became smaller and paler while the remaining thallus continued to be progressively affected, leaving behind necrotic thallus and the remains of rhizines or cilia (Fig. 8a, 8b). The host rhizines connect the thallus to the substrate and are almost indistinguishable from cilia which can also provide anchorage should they contact the substrate (Clark & Crabtree, 2022). Cilia bridge the thalli, connecting them and acting as spacers (Fig. 8c, 8d).

There is no evidence to suggest mutualism or commensalism and no indication that infection with *Ill. christiansenii* is in any way beneficial to the *Physcia* host. *Ill. christiansenii* is, on the one hand, at least mildly parasitic, causing discolouration of the thallus, and on the other hand, it appears to be saprophytic on the algal/necrotic crusts. It may attack infected or damaged thalli, but it is also strongly associated with *Physcia* species and spreads progressively across the healthy thallus. If the initial cause were poor lichen health due to some other pathogen or chemical damage preceding it, some visible evidence of this might be expected.

Remains of rhizines or cilia were observed after the thallus had been degraded. Cilia and rhizines comprise only fungal material which suggests that the LF is initially attacking the trebouxioid photobiont. This is also indicated by the discoloration of the thallus caused by the infection.

The ciliate inter-thalline links could enable the LF to enter neighbouring thallus branches directly, causing a rapid progressive spread of infection of the type observed. *Ill. christiansenii* was also recorded on non-ciliate *Physcia* species, but its success with its two most common *Physcia* hosts might be linked to inter-thallus spreading of infection via cilia.

Damage to the host thallus continued through the summer, irrespective of the absence of cirrhi, indicating that the parasitic activity continues all year.

Conclusion The relationship best fits the case of a parasite destroying parts of the thallus and then persisting as a saprobe on the residual necrotic thallus. In the saprobe stage, cirrhi are produced during the reproductive season but so far cirrhi have not been seen erupting from the thalli. During the reproductive season, cirrhi and thallus discolouration are observed side-by-side, but only the thallus damage proceeds in the off-season.

Figure 7 Top: Degradation of *Physcia tenella* thallus on a painted metal gate bar at Site 3 over 6 months: photographs were taken from September 2022 to March 2023. On this thallus, pink cirrhi reappeared in early October and can be seen on the November and March pictures. Some of the *Xanthoria parietina* overgrowing the *P. tenella* also appears to have lost its hold as the *Physcia* supporting it was destroyed. The bar indicates the approximate alignment of the photographs.

Photos © D.M. Napier





Left: Degradation of *Physcia adscendens* thallus on a senescent *Fraxinus* twig at Site 2 over 12 months. Photographs were taken monthly in the course of 2022.

The pink cirrhi were not observed from February until they reappeared in September. On this December photograph they are too small to be visible (see Fig. 8 for detail).

The bar indicates the approximate alignment of the photographs.

Photos © A.M. Claypole

Figure 8 (a) Site 2, 12 November 2022 cirrhi emerging in areas where thallus had been destroyed six months earlier.

(b) The same, 09 December 2022. The arrows point to the same group of cirrhi. A further strip of thallus (almost 1 cm across) has been destroyed, leaving more necrotic thallus with the remains of rhizines or cilia. Some cirrhi are no longer visible and others are smaller and paler.

(c and d) Cilia and rhizines anchor the thallus to the substrate and cilia bridge the thalli, both connecting them and holding them apart.



(b)













Photos © A.M. Claypole

Two questions arising

Why did Ill. christiansenii appear so suddenly in 2012?

The literature offers two explanations but little evidence for either.

Firstly, a growing awareness of LFs may have stimulated interest and recording. Spier (2001) argues that this is unlikely to be the case for *Ill. christiansenii* because the bright pink colour is difficult to overlook. He cites the sudden appearance of *Ill. christiansenii* in 1998 in the Netherlands on *Quercus*. These trees are one of the main phorophytes of *P. tenella* and were part of a long-term field study. Bright pink cirrhi could not have been overlooked for almost 10 years. In the UK, there was a similar sharp rise in sightings in 2012, although *Ill. christiansenii* had been recorded since 1985.

The second suggestion is that the rise in sightings may have resulted from changes in environmental pollution. Falling SO₂ pollution correlated with effects on host lichen health, LF sightings and the number of LF species. Many LFs, including *Ill. christiansenii*, appeared to have been favoured by the drop in SO₂ pollution. Increasing nitrogen pollution from agriculture and catalytic converters in both rural and urban areas of the UK and Europe correlated with an increase in nitrophilic lichen species such as *Physcia* and *Xanthoria*. Spier (*ibid*) suggests that the dramatic rise in *Ill. christiansenii* may have been a result of this massive increase in *P. tenella*. However, there was never any shortage of this host since most of the nitrophilic lichen species has been attributed to increased bark pH (van Herk, 2001) which may also have favoured the *Ill. christiansenii* cirrhi since they arise in close proximity to the bark.

What limits the reproductive season and has this caused the phenology to change?

Whatever kickstarts the production of cirrhi in autumn is not necessarily what stops it in spring. There are three main interrelated physical factors to consider: light, humidity and temperature. The longer the days, the warmer. The warmer the air, the drier. The cirrhi are poikilohydric which means their water status is completely dependent on the environment. They cannot release their spores when dry. The observed reproductive period is colder, more humid and has shorter days than the inactive period.

Another aspect of light is daylength (photoperiod). The majority of recorded host lichens are on deciduous trees. Both the onset and breaking of dormancy in trees are primarily controlled by daylength and temperature, albeit in different ways. The development/loss of a leaf canopy may affect the development of cirrhi, either directly through changes in shading or the humidity surrounding the bark, or indirectly through changes in the metabolism of the tree. A shorter phorophyte dormancy might explain the shortening of the reproductive season of the LF.

Records on Nature's Calendar (Woodland Trust and the Centre for Ecology and Hydrology) indicate a later autumn and an earlier spring in the UK (Proceedings of the Royal Society B, 2022). A phenological study (Menzel *et al.*, 2006) revealed significant effects of climate change on the recorded phenology of many plant species across Europe. Species' phenology responded to the temperature of the preceding months, showing an advance of spring and a delay of autumn. It would not be surprising, therefore, to find effects on the *Physcia* host lichen, the phorophytes, or even *Ill. christiansenii* itself.

Summary

The picture emerging is of a fungus associated with *Physcia*, *Phaeophyscia* and *Physconia* species in nutrient-rich communities. *Ill. christiansenii* is most commonly, but not exclusively, found on the bark of certain deciduous trees. An asexual reproductive season produces the bright pink cirrhi observed in the autumn and winter months, but the reproductive season has become shorter. The evidence points to a fungus with two growth stages: a parasitic lichenicolous stage, and a saprobe stage. This model resolves many of the apparently conflicting reports in the literature.

These studies also debunked the myth that lichenologists prefer to foray in the winter.

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