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Hyperphyscia lucida (Physciaceae, lichenized Ascomycota), a new species from willow forests in the Biesbosch, the Netherlands

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Hyperphyscia lucida is described as a new lichen species from the Netherlands on morphological grounds. It most closely resembles *H. adglutinata*, but differs by a whiter grey thallus, confluent or laterally imbricate, mostly flat and closely appressed, shiny lobes, a transparent prothallus, and groups of laminal pustules that develop into finely granular to coarsely isidioid soredia. *Hyperphyscia lucida* was found in 2020 in an area of approximately 1 km^2 in the freshwater tidal area the Biesbosch. Thalli were found on 14 *Salix* trees in the southwest of two ca 60-year-old willow forests, together with a. o. *Hyperphyscia adglutinata* (with apothecia), *Phaeophyscia orbicularis*, *Xanthoria parietina* and *Hypnum cupressiforme*. Further interesting companions include *Porina byssophila*, *Physciella chloantha* and *Strangospora deplanata*.

Keywords: climate change, Hyperphysica, lichens, new species, phylogenetic, *taxonomy*

The Biesbosch is a freshwater tidal area in the basin of the rivers Meuse and Rhine in the southwest of the Netherlands. The area originated in 1421 when a major flood, the 'Sint-Elisabethsvloed' initiated the destruction of a large polder area called 'Groote Waard'. An inland sea of approximately 300 km^2 of water resulted. Since then, river sediments slowly again transformed this into land. The different stages of land development were always strongly influenced by man, with e.g. fishery in open water, rush and reed cultures on mud and sand flats, willow coppices in so-called 'grienden', and agriculture in the newly regained polders, on the highest grounds embanked by dikes. Formerly, a tidal amplitude of ca 2 m existed. Due to the construction of the Haringvlietdam in 1970 the direct connection with the sea was blocked. Since then only an amplitude of 20–40 cm, and locally 80 cm remained. Since 1950 and especially after 1970 for economic reasons almost all willow coppices in the Biesbosch have been abandoned and developed into more natural willow forests. In 1994 parts of the wetlands with high natural and recreational value were designated as a Natural Park.

The bryophyte and lichen flora of these extensive woodlands have been monitored thoroughly since 1969, starting with Brand and During (1972) and van Zanten and During (1970), and since 1983 by the author (van der Pluijm 1995).

In the winter of 2020, a peculiar *Hyperphyscia* was found on the island 'Middelste Jannezand' (Fig. 1). A white grey, shiny thallus and relatively large dimensions were the first to attract attention. A constant set of characters clearly distinguished the taxon from the locally common *Hyperphyscia adglutinata* (Flörke) H. Mayrhofer & Poelt. Further fieldwork revealed two local populations of the 'new' lichen on many trees. In mixed populations with *H. adglutinata* each thallus could be attributed either to *H. adglutinata* or to the new lichen, thus no intermediate forms were observed. In Europe *H. adglutinata* is the only *Hyperphyscia* known to occur. Also, the literature on species of *Hyperphyscia* worldwide did not reveal any satisfactory name, and therefore on morphological grounds the taxon is here described as a new species.

Material and methods

Specimens were examined with a stereomicroscope and a light microscope. Habitus photographs were taken with an Olympus TG4 digital compact camera, microscope photos with a Canon Ixus 70 on a tripod, placed before the eyepiece of the microscope. Sections were hand cut with a razor blade. Chemical reactions were tested with K (10% KOH), C (sodium hypochlorite, commercial bleach) and P (paraphenylenediamine, crystals in alcohol).

The species

Hyperphyscia lucida van der Pluijm, sp. nov. (Fig. 2–5) MycoBank nr.: MB 837342.

Figure 1. The Netherlands, freshwater tidal area Biesbosch, view on island 'Middelste Jannezand', 27-3-2020, type location of *Hyperphyscia lucida* sp. nov. (and *Chaenotheca biesboschii,* Tibell et al. 2019).

Diagnosis

Hyperphyscia with a small, white grey to grey thallus. Marginal lobes confluent, laterally imbricate or with laterally upturned margins, 0.2–1.5 mm wide, mostly flat and closely appressed, shiny and with a transparent prothallus, sometimes with upturned margins, rhizines absent. Lobes with groups of pustules, laminal or on ridges of lobe folds. Soralia developing from pustules, with irregular outline, soredia finely granular to secondarily, coarsely isidioid. Medulla white. Chemical reactions K−, C− and P−.

Type: the Netherlands, prov. Noord-Brabant, Werkendam, Biesbosch, Middelste Jannezand, GPS 51.7306N, 4.8483E, alt. 1 m a.s.l., on vertical, ca 50-year old *Salix*-stem, 2 m high, in freshwater tidal willow forest, 'tree 5'. Leg. van der Pluijm 3641a, 5-3-2020, Herbarium L.

Etymology

The specific epithet refers to the often remarkably shiny upper cortex of young thallus lobes and the shiny prothallus.

Description

Thallus foliose to subcrustose, corticolous, small to very small, 0.5–2 cm in diameter, sometimes thalli confluent, white grey or grey, sometimes dark grey, green when moist, mostly closely appressed from centre to edge and cannot be removed from the surface without damage, towards the centre often with obliquely transverse or radially arranged folds. Photobiont trebouxioid, 3–20 µm. Lobes irregular, broadest near the tips, strongly (sometimes irregularly pinnately) sublobed, contiguous, laterally imbricate or with laterally raised margins between neighbouring lobes, variable in width, 0.2–1.5 mm wide, marginal lobes in outline often suborbicular or somewhat broader than long, with a shiny surface, epruinose, mostly closely appressed and flat, sometimes the extreme margin darker in colour, sometimes with upturned outer margins with a white underside, seldom lobes loosely attached and partly overgrowing mosses. Appressed lobes mostly with a translucent or whitish, shiny prothallus film, ca 0.1–0.25 mm wide. Moist prothallus of long, branched, cellular fungal hyphae, ca 3 µm broad,

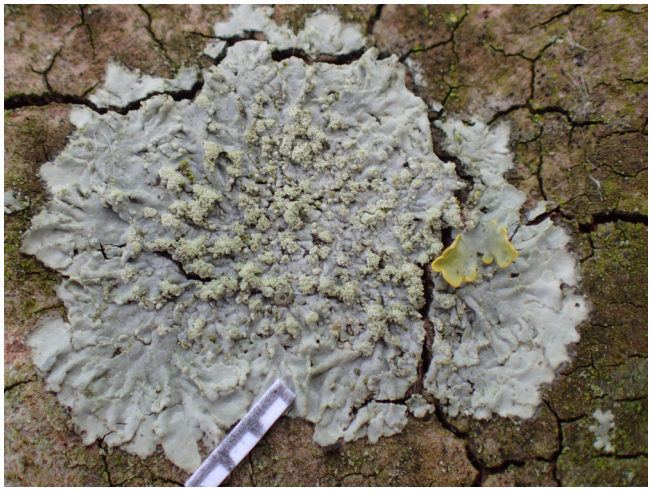

Figure 2. Habitus *Hyperphyscia lucida*, holotype, thallus 13 × 11 mm. With white grey, flat, closely appressed, rather wide, 0.5–1 mm broad lobes, with a shiny surface, a translucent, shiny prothallus zone and diffuse, farinose and isidioid soralia, originating from mostly laminal pustules (bar line in mm).

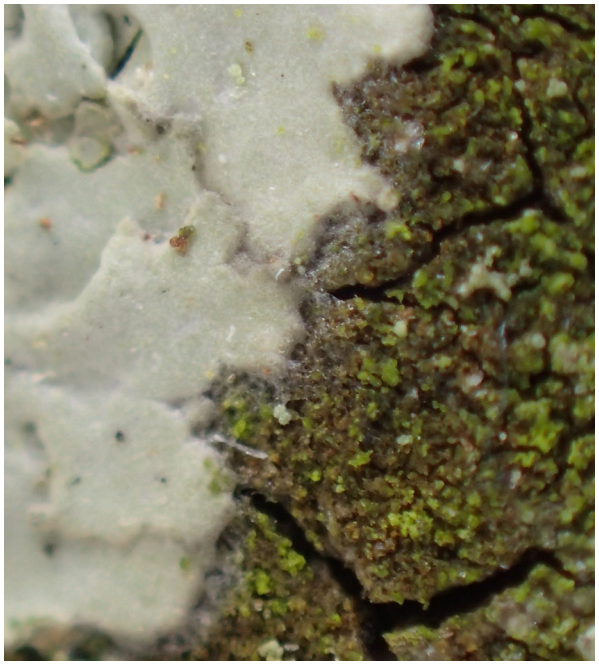

Figure 3. Detail *Hyperphyscia lucida*, holotype. With flat outer lobes, closely appressed, with a shiny, translucent prothallus, ca 0.2 mm wide.

embedded in a hyaline, gelatinous matrix. On the underside of lobes with upturned margins, the prothallus film is sometimes submarginal and hidden below the margin. In herbarium specimens the prothallus can stick out as a membrane after deformation of the bark sample by drying out.

Young lobes with groups of pustules (ca 5–20), laminal, or on the ridges of folds (in fact also laminal), or seldom also marginal. Pustules ca 0.1–0.15 mm in diameter, with a cracked cortex, often present on parts of thallus only. Soralia principally laminal, developing from pustules, green grey, diffuse, not regularly delimited, with finely granular goniocysts on a partly exposed, woolly medulla. Goniocysts

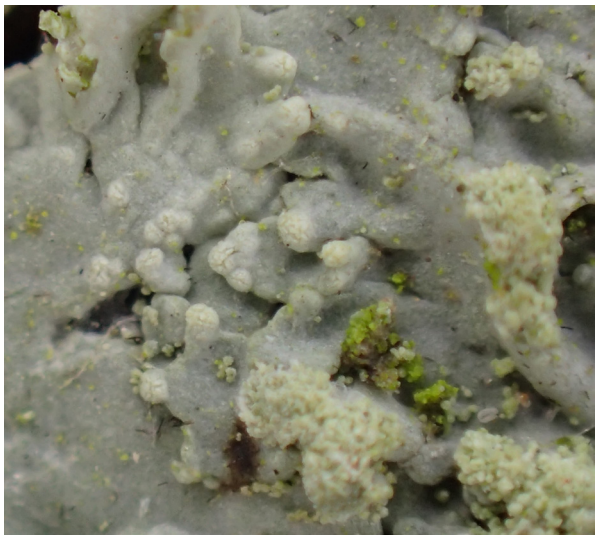

Figure 4. Detail *Hyperphyscia lucida*, holotype. Grey lobes with many, aggregated, laminal and some marginal, white grey pustules, ca 0.15 mm wide, with a cracked cortex layer.

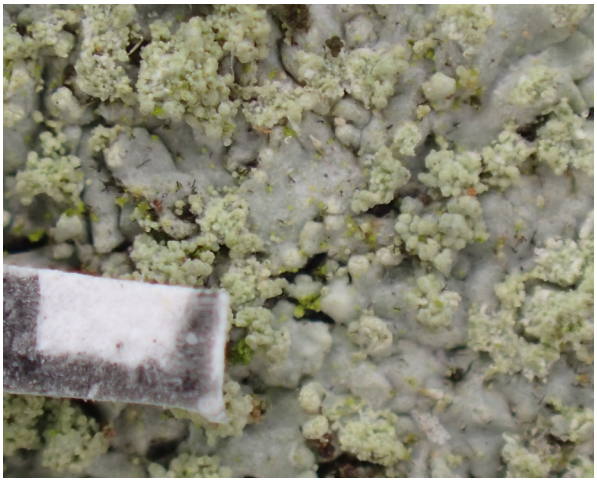

Figure 5. Detail *Hyperphyscia lucida*, holotype, central part of thallus, with irregular, green grey soralia, with farinose soredia (goniocysts) and with coarse, secondarily isidioid soredia intermixed, and with laminal pustules (bar line in mm).

ca 20–50 µm, with inner green photobiont cells surrounded by one layer of hyaline spherical, relatively large fungal cells of 3–8 µm, sometimes hyaline outer cells in chains of 2–4. In exposed habitats the pustules on the thallus lobes often develop into white grey, yellow grey or grey, firm 'soralia' and mostly contain relatively few, coarse, spherical isidioid soredia or somewhat flattened phyllidia, 50–250 µm in diameter. These isidia-like structures have a paraplectenchymatous, hyaline outer layer, with small, 2–4 µm wide fungal cells. Sometimes phyllidia grow out as flattened, closely appressed, 0.25–0.4 mm wide lobules over older thallus lobes. The end lobes may also develop many marginal, young lobes that grow back towards the thallus centre, appressed on older lobes.

Thallus thin, ca 0.07–0.15 mm, often thicker, up to 0.3 mm (moist) near margins, sometimes older thalli up to 0.5 mm thick, by stacking of thallus lobes and isidioids. Upper cortex paraplectenchymatous, ca 15–20 µm thick, with multiple layers of rounded cells of 2–6 µm (Fig. 6), photobiont layer beneath of the same width or somewhat wider. Medulla white, mostly compact, but at thallus margins (moist) often extremely lax and embedded in a gelatinous matrix (Fig. 7), forming a thick layer that merges into the prothallus. Lower cortex absent, indistinct or prosoplectenchymatous (Fig. 6) on laminal thallus, absent on the underside of lobe margins and ascending thallus lobes (Fig. 7). Rhizines absent.

Apothecia and pycnidia not observed.

Chemistry

Thallus and medulla K−, C− and P−.

Distribution

Known only from the Netherlands, prov. Noord-Brabant, Biesbosch, in two willow forests, 'Middelste Jannezand' and 'Aakvlaai' (Fig. 8).

Ecology

On *Salix alba* L. in ca 60-year-old willow forests in a former freshwater tidal area. On old stems and on vertical, young branches of fallen down, rejuvenating willows, 0.4–3 m high.

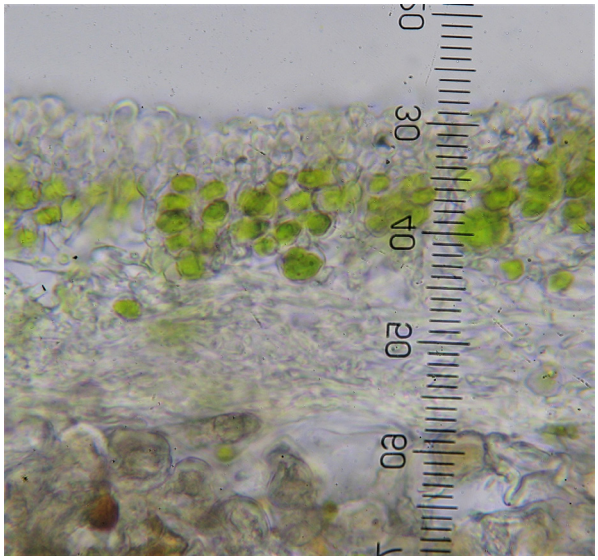

Figure 6. Part of longitudinal section of thin (ca 90 µm) laminal thallus lobe (not margin) of *Hyperphyscia lucida*, coll. v. d. Pluijm 3620. 1 divide = 2.8 µm. With paraplectenchymatous upper cortex, photobiont layer, medulla and indistinct prosoplectenchymatous lower cortex.

Taxonomic discussion

Species of the genus *Hyperphyscia* Müll. Arg. are characterised by a relatively small, closely adnate, greyish to brown, foliose thallus, with a paraplectenchymatous upper cortex, lacking atranorin (reaction K−) and an indistinct or prosoplectenchymatous lower cortex, (almost) without rhizines. Ascospores are mostly of the *Physcia-* or *Pachysporaria-*type and pycnospores are filiform and usually over 15 µm long (Moberg 1987). In contrast, species of other, related genera of the Physciaceae, e.g. *Phaeophyscia* Moberg and *Physciella* Essl. are less 'glued' to the surface, with rhizines on the underside and have a thallus with a well-developed lower cortex (paraplectenchymatous in *Phaeophyscia*, prosoplectenchymatous in *Physciella*). Pycnospores are ellipsoid and mostly under 6 µm long (Liu and Hur 2019).

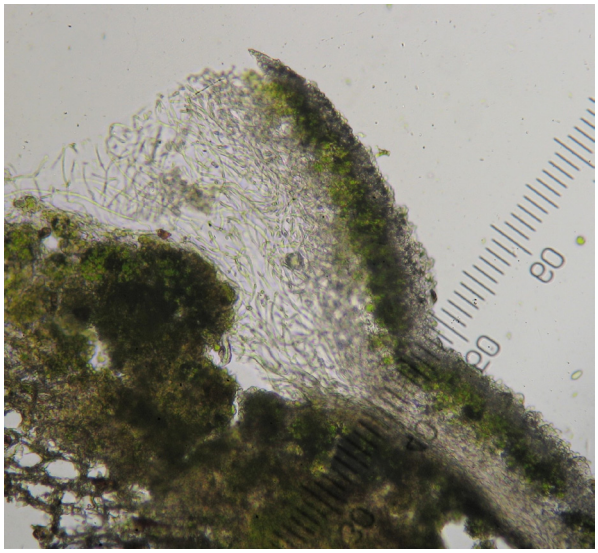

Figure 7. Longitudinal section of lobe margin of *Hyperphyscia lucida*, overgrowing algae on bark, coll. v. d. Pluijm 3620. 1 divide = 11.6 µm. Notice thallus margin thick (moist, ca 0.3 mm), much thicker than laminal thallus (0.1 mm), without lower cortex, with a very lax medulla merging into a prothallus beyond the thallus lobe. The boundary of the hyaline, gelatinous matrix surrounding the hyphae is hardly visible.

Because of thallus morphology and anatomy, and negative K-reaction of the upper cortex, the new taxon clearly belongs in *Hyperphyscia*. The shape and size of the conidia could unfortunately not yet be checked, since no thalli with pycnidia (or apothecia) have been found up to now.

Comparison of the new Dutch taxon with species of the genus *Hyperphyscia*

According to Scutari (1991) the genus *Hyperphyscia* until then comprised approximately 13 species, mainly from the tropics and subtropics. She added three species, two of which via new combinations. Since then, some six more species or new combinations have been described by Scutari (1997), Esslinger et al. (2012), Filippini et al. (2015) and Kondratyuk et al. (2018). The Index Fungorum (2020) lists 23 species. Almost all these species are included in the world key for *Hyperphyscia* in Sipman (2002). At first with this key and additional literature an attempt was made to attribute an existing name of *Hyperphyscia* to the Dutch specimens. From the relatively large group of species of *Hyperphyscia* with soralia, after exclusion of the species with an orange to red medulla, *H. adglutinata*, *H. cochlearis* Scutari, *H. confusa* Essl., C.A. Morse & S. Leavitt, *H. minor* (Fée) D.D. Awasthi, *H. mobergii* Kalb, *H. oxneri* S.Y. Kondr. & Hur, *H. pruinosa* Moberg and *H. variabilis* Scutari remained as candidates. However, to my opinion the new Dutch taxon differs basically from all these species, except *H. adglutinata* by the laminal soralia originating from pustules.

On a worldwide scale for long *Hyperphyscia adglutinata* was considered a very variable species. Moberg (1987) e.g. still had a wide species concept and reported specimens from East Africa with lobes up to 2 mm broad and ascending tips. However, in recent decades it has become clear that part of this 'variation' was caused by the inclusion of yet undescribed species. So, according to Scutari (1997), after revision of numerous collections, including collections from East Africa (from UPS), *H. adglutinata* appears to be a homogeneous, cosmopolitan species, characterised by a small brownish thallus, narrow flat lobes up to 0.4–0.5 mm broad and laminal soralia. She emphasised that most of the atypical specimens at UPS referred to as *H. adglutinata* (at least one collection from Kenya, East Africa, Moberg 4466a is mentioned in the representative specimens examined) belong to *H. cochlearis*, a species she then newly describes. *Hyperphyscia cochlearis* and also *H. variabilis* (Scutari 1991) were described as separate species from *H. adglutinata*, partly because of their relatively larger size and marginal, not laminal soralia. Also, with these species the soralia are initially punctiform and later become farinose. They do not seem to arise from pustules, a constant character of the Dutch taxon. Also, coarse isidioid soralia are not mentioned for *H. variabilis* and *H. cochlearis*. The delimitation of *H. adglutinata* in North America was further narrowed down by the description of *H. confusa* (Esslinger et al. 2012), with

Figure 8. Distribution of *Hyperphyscia lucida* (red dots) in the Netherlands, Biesbosch, in two freshwater tidal willow forests, 'Middelste Jannezand' (north) and 'Aakvlaai' (south).

marginal instead of laminal soralia. To complete the discussion on 'non'-candidates, *H. pruinosa* and *H. mobergii* also differ by having marginal soralia. With *H. oxneri* thallus lobes are nearly absent (Kondratyuk et al. 2018) and *H. minor* has a black prothallus and a medulla spotted with orange pigments.

Only *H. adglutinata* s.s. also has principally laminal soralia that originate from pustules. The multiple differences between this species and the new Dutch taxon are outlined in the next paragraph and these warrant the description of a new species *Hyperphyscia lucida*.

Comparison of *Hyperphyscia lucida* with *H. adglutinata* in the Netherlands

On the trees in the Biesbosch with *Hyperphyscia lucida* always also *H. adglutinata* was present. Both species often even grow intermixed (Fig. 9–10), but individual thalli could always be attributed to one or the other, and no ambiguous, 'intermediate' thalli were found. Mostly, *H. lucida* can be recognised with a hand lens in the field, but sometimes a stereomicroscope is useful for checking finer details. *Hyperphyscia lucida* often stands out by a slightly lighter shade of grey of the thallus (Fig. 10) than *H. adglutinata*. Typically, it is white grey, but in habitats more strongly exposed to the sun, it can be grey to even dark grey.

Overall thallus size of both species is frequently similar, but *H. lucida* often has relatively broader, up to 1.5 mm wide lobes, whereas those of *H. adglutinata* are mostly only 0.2–0.5 mm wide. However, also with *H. lucida* thalli with minute end lobes can occur. In that case the narrow lobes are shiny, strikingly flat, often laterally imbricate and mostly rimmed with a varnish-like prothallus, up to ca 0.2 mm wide (Fig. 11 top). *Hyperphyscia adglutinata* has duller, mostly discrete or contiguous, slightly convex end lobes, without a clearly discernible prothallus, or the underlying hyphae of attachment only fringe out marginally (Fig. 11 below), or fragments of a prothallus are only developed between parallel end lobes. However, sometimes thalli of *H. adglutinata* are grazed by e.g. snails. When the outermost edges of the thalli are gnawed away, a narrow, shiny band of – normally underlying – hyphae for attachment can be exposed. These damaged thalli parts are not to be confused with a real prothallus.

Thalli of *H. lucida* and *H. adglutinata* are often of the same size, but *H. lucida* seems to have a greater inclination for 'lateral' growth, especially with white grey morphs in less exposed habitats. This results in laterally imbricating lobes or neighbouring lobes having upright lateral margins, and – before lobe furcations – an uplifting of the thallus into folds. The end lobes are also often isodiametric or broader than long. *Hyperphyscia adglutinata* on the other hand mostly has discrete or contiguous lobes, that are usually longer than broad, and an inner thallus less frequently with folds.

Sometimes on older thalli of *Hyperphyscia lucida* black patches can be found between the inner grey lobes. These are not a real prothallus, since in cross sections these patches mostly appear to be necrotic remnants of older thallus lobes, not felts of viable, young fungal hyphae. Young lobes not only grow outwards of the thallus centre, but frequently also inwards over older lobes that can die off in the process.

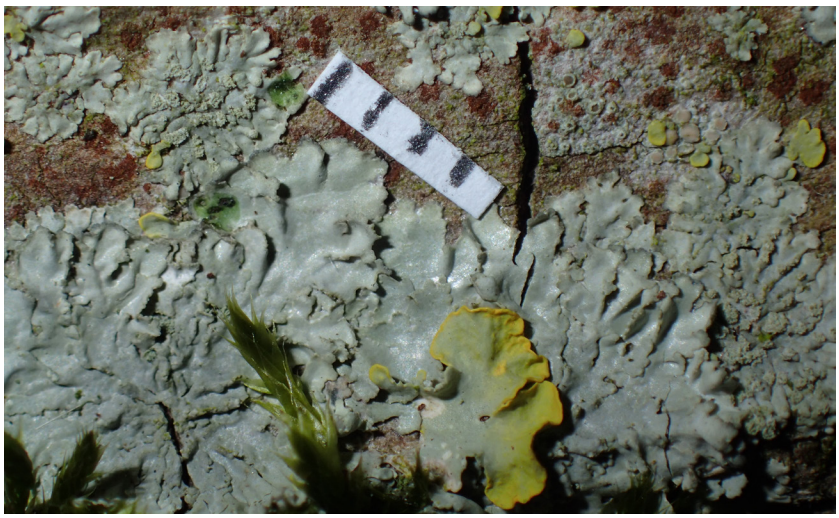

Figure 9. Young, luxurious thallus of *Hyperphyscia lucida* (below) intermixed with, and overgrowing *H. adglutinata*, coll. v. d. Pluijm 3620. Notice this morph of *H. lucida* has a slightly whiter thallus than *H. adglutinata*, with some radially arranged folds; thallus lobes are broad, shiny (photo with flashlight), some with laterally upturned margins, with a translucent prothallus, still almost without soralia and with only a few pustules. *Hyperphyscia adglutinata* (above) has thalli with narrower, more grey, dull lobes, without a prothallus and already has rounded, laminal soralia (bar line in mm).

An 'afterthallus' would be a better term for this phenomenon. Real prothallus in this species can be observed as a shiny, translucent or whitish fungal film on the bark that is eventually grown over by a complete thallus. It can also be found on older thallus lobes, on the margins of overgrowing, appressed, young thallus lobes.

Hyperphyscia lucida and *H. adglutinata* also differ in soralia arrangement, morphology and development. In both species the soralia originate from pustules of which the cortex cracks open (Fig. 4). *Hyperphyscia adglutinata* has solitary, mostly laminal or submarginal pustules on young lobes

Figure 10. Mature thallus of *Hyperphyscia lucida* (left) overgrowing thallus of *H. adglutinata* (right), coll. v. d. Pluijm 3641b (isotype). Notice the slightly whiter grey thallus of *H. lucida*, with flat, confluent lobes, with numerous pustules and with diffuse soralia. *Hyperphyscia adglutinata* with thallus lobes slightly discrete, greyer and somewhat convex, with discrete, rounded, finely farinose soralia, often surrounded by white cortex scales (bar line in mm).

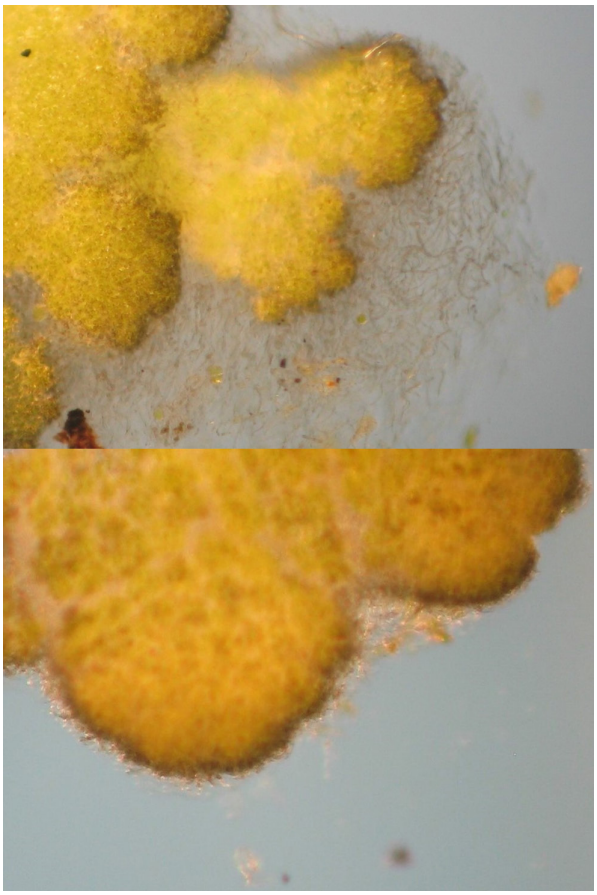

Figure 11. Comparison of thallus lobe margins of *Hyperphyscia lucida* (top, coll. v. d. Pluijm 3650b) and *H. adglutinata* (below, coll. v. d. Pluijm 3634). *Hyperphyscia lucida* with a prothallus film, ca 0.2 mm wide, of branched, cellular fungal hyphae, *H. adglutinata* almost without prothallus, only with a narrow, protruding fringe of hyphae of attachment.

(pustules sometimes on some lobes only). These then develop into solitary, flat or hemispherical, ca 0.15–0.35 mm broad soralia. Older soralia are often abraded (especially in herbarium convolutes), circular, crateriform and surrounded by a fragmented ring of white, upright or reflexed cortex scales (Fig. 10). In the centre of older thalli, the soralia may become confluent. *Hyperphyscia lucida* however, often has multiple (up to 10 or 20, Fig. 4, 10) pustules aggregated together, mostly on the lamina of lobes, or on ridges of thallus folds. From the very start, confluent, oblong or diffuse soralia then develop. With *H. lucida* also some white cortex scales can be found at the edges of abraded soralia, but these are not arranged in neat rings. The soredia of *H. adglutinata* and *H. lucida* mostly vary in diameter from 20 to 50 µm. When examined microscopically (Fig. 12), I think they should be better categorised as goniocysts, defined by Büdel and Scheidegger (2008) as 'granular thalli with external monolayered paraplectenchymatous fungal plectenchyme and numerous photobiont cells.' The term 'true' soredia, as 'photobiont cells enveloped by a mantle of loose hyphae' does not apply well here. Although *Hyperphyscia lucida* is primarily a sorediate species, the green grey soralia often become secondarily isidioid (Fig. 5), and in exposed habitats they often contain a relatively small number of large, grey to dark grey or blackish, spherical or flattened isidioid soredia ('secondarily corticate protuberances produced in soralia-like clusters' in Büdel and Scheidegger 2008), surrounded by a paler, grey or yellow grey mass of agglutinated goniocysts (Fig. 13). These 'isidioid soralia' have a firmer texture than normal farinose soralia, and more or less shield off the underlying medulla as a thin crust. In exposed sites *Hyperphyscia adglutinata* often also has darker grey soralia, but mostly the goniocysts do not grow out into large isidioid soredia.

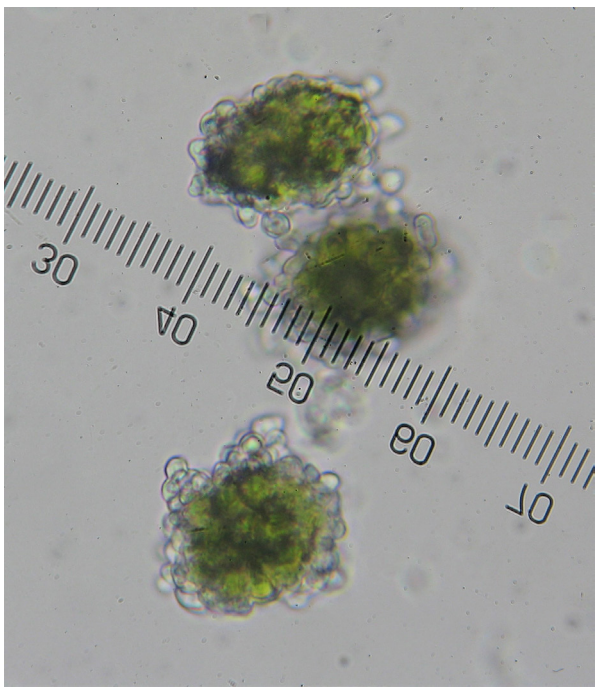

Figure 12. *Hyperphyscia lucida*, coll. v. d. Pluijm 3641b (isotype), Goniocysts from soralia, with outer, one cell layer of paraplectenchymatous, spherical fungal cells, sometimes cells in short chains. 1 divide = 2.8 µm.

Key for *Hyperphyscia*-species with laminal soralia and pustules.

1. Thallus white grey, grey or dark grey. Lobes contiguous, laterally imbricate or with laterally upturned margins, end lobes 0.2–1.5 mm wide, flat or with upturned outer margins, shiny, with prothallus. Pustules numerous, aggregated. Soralia irregular or diffuse, soredia finely granular, becoming secondarily coarsely isidioid……
…….*Hyperphyscia lucida*
– Thallus grey to dark grey or brown grey. Lobes mostly discrete or contiguous, end lobes 0.2–0.5 mm wide, slightly convex, dull, without prothallus. Pustules singular. Soralia circular, later becoming confluent, soredia finely granular……...*Hyperphyscia adglutinata*

Distribution of *Hyperphyscia lucida and H. adglutinata* in the Netherlands

The distribution of (macro)lichens in the Netherlands is well documented, with data going back to the beginning of the 19th century (NDFF Verspreidingsatlas Korstmossen 2020). The information is presented on a grid of 1674 square cells of 5 × 5 km, and especially after 1970 a fair degree of national coverage is achieved. For long in the Netherlands *Hyperphyscia adglutinata* was not rare in coastal locations, but it had become very rare (present in less than 1% of the grid cells) in the second half of the 20th century (<www.verspreidingsatlas.nl/4496>), probably because of the impact of air pollution with sulphur dioxide (SO_2). However, since ca 1990 the species has expanded its range spectacularly, and in the decade of 2010 until 2020 it has been recorded in no less than 60% of the grid cells of the country. Of course, air quality (as for SO_2) has improved since, but certainly this (sub)

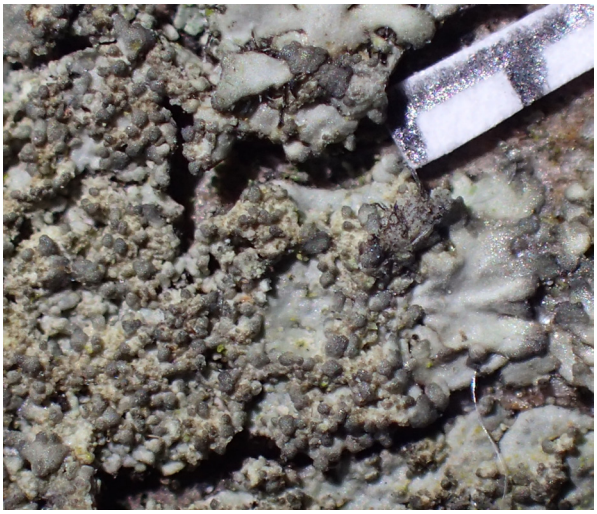

Figure 13. Thallus of *Hyperphyscia lucida*, in exposed habitat, coll. v. d. Pluijm 3650a. Thallus 0.3–0.5 mm thick, grey with older, 'crusty', yellow grey soralia containing few, large, dark grey or blackish, spherical or somewhat flattened isidioid soredia (bar line in mm).

Table 1. Accompanying lichens and bryophytes of *Hyperphyscia lucida* in willowforests in the Biesbosch in the Netherlands, in order of presence. Relevés of ca 1–10 dm² on 14 willow trees in the direct vicinity of thalli of *H. lucida*. Only presence, not abundance was noted. Holotype and isotypes collected on tree '5'. Abbreviations: M.J.– 'Middelste Jannezand', Aak. – 'Aakvlaai'. R.b. – vertical regeneration branch. ! = with capsules, apothecia or perithecia. All recorded in spring of 2020, further, extended data (e.g. GPS) via <www.verspreidingsatlas.nl/korstmossen>.

Accompanying species of Hyperphyscia lucida in the Biesbosch, in order of presence														
Number of tree	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Location	M.J.	M.J.	M.J.	M.J.	M.J.	M.J.	M.J.	M.J.	M.J.	Aak	Aak	Aak	Aak	Aak
Habitat	R.b.	Stem	Stem	Stem	Stem	Stem	Stem	Stem	R.b.	Stem	Stem	Stem	Stem	R.b.
Height (m)	0.7–2	1–1.9	1.8	1.6–2	2	0.4–1	3–3.2	1.8–2	0.6-1.2	1	1–1.8	1.6–2.2	2	1–1.3
Diameter (cm)	13	60	35	20	35	60	35	40	15	30	40	50	45	15
Herb.-nr. v.d. Pluijm	3650	3620	3645		3641	3640			3653	3688	3678	3675	3676	3685
Accompanying lichens and bryophytes (! with capsules, apothecia or perithecia):														
Hyperphyscia adglutinata	x	x!	x	x	x	x	x	x!	x	x	x!	x	x	x
Phaeophyscia orbicularis	x	x	x	x	x	x	x	x	x	x!	x	x	x	x
Xanthoria parietina	x!	x!	x!	x!	x!	x!	x!	x!	x!		x!	x!	x!	x!
Hypnum cupressiforme	x!	x	x	x	x	x	x	x	x		x	x		x
Lecania cyrtella		x!	x!	x!	x!	x!	x!	x!	x!				x!	
Trentepohlia spec. (Algae)	x	x	x			x	x	x			x		x	
Porina byssophila			x!			x!				x!	x!	x!	x!	x!
Anisomeridium polypori		x			x		x	x		x			x	
Lepraria finkii			x	x	x	x	x		x					
Physcia adscendens		x	x	x		x	x				x			
Strigula taylorii	x		x		x				x		x		x	
Syntrichia papillosa	x				x				x			x		x
Alyxoria varia	x!		x!						x!			x!		x!
Physciella chloantha	x		x						x!				x	
Orthotrichum affine	x!								x					x
Caloplaca obscurella		x									x	x		
Opegrapha vermicellifera			x			x			x					
Physconia grisea	x								x			x		
Homalothecium sericeum				x	x									
Leskea polycarpa	x								x					
Orthotrichum diaphanum	x!							x!						
Orthotrichum obtusifolium	x								x					
Orthotrichum tenellum	x!													x
Pylaisia polyantha	x								x!					
Lecanora expallens											x	x		
Pseudoschismat. rufescens										x!	x!			
Amblystegium serpens	x													
Cryphaea heteromalla	x													
Syntrichia laevipila														x
Zygodon conoideus								x						
Zygodon viridissimus									x					
Frullania dilatata									x					
Radula complanata	x													
Candelaria concolor	x													
Lecania naegelii											x!			
Lecanora hagenii		x!												
Lecidella elaeochroma									x!					
Opegrapha vulgata											x!			
Parmelia sulcata		x												
Ramalina farinacea											x			
Strangospora deplanata	x													

tropical species will also have benefited from a nowadays warmer climate. As for the Biesbosch area, *H. adglutinata* was first discovered in 1999 and has become very common since. At first only thalli with soralia were observed, but since 2018 frequently also such with apothecia.

So far *Hyperphyscia lucida* has been found in the Biesbosch in an area of about 1 km^2 (Fig. 8), in two separate populations. Both forests here have been thoroughly monitored, but *H. lucida* up till now seems restricted to the southwestern parts, close to the riverbank. With the upcoming summer of 2020, with the stinging nettle *Urtica dioica* L. growing into impenetrable, 2–3 m high stands, other potentially favourable locations in the National Park could not yet be visited.

Ecology of *Hyperphyscia lucida* and *H. adglutinata* in the Netherlands

In the Netherlands *Hyperphyscia adglutinata* is found on nutrient-rich or eutrophicated bark of young and old trees, along roads, in villages, on (farm)yards, in parks and in moist forests (van Herk et al. 2017). As a (sub)tropical species it can tolerate high temperatures. As noted in Smith et al. (2009) its habitats are often also sheltered or shaded. Comparable ecological parameters (perhaps even in an extremer degree) seem to hold for *Hyperphyscia lucida* in the Biesbosch, and until now it also always has been found in company of *H. adglutinata*.

In dense willow forests in the Biesbosch mostly mosses dominate over lichens. After ca 20 years of succession (starting as abandoned coppice woods, 'grienden'), thick mats of pleurocarpous mosses like *Brachythecium rutabulum* (Hedw.) Schimp. and *Hypnum cupressiforme* Hedw. can often grow up to 8 m high on stems (van der Pluijm 1995) and then compete with other bryophytes and lichens. With further aging (the 'Middelste Jannezand' and 'Aakvlaai' forests are ca 60 years old) these moss mats are often partly destroyed by foraging birds or by forces of wind or gravity. In recent decades, with a significantly warmer climate, in prolonged dry periods in spring and early summer, moss mats on trunks are regularly scorched and bleached by the sun. Inside the willow forests this can result in an extremely species-poor epiphyte vegetation on shaded, old willows, through a continuous regeneration in fall and winter of left behind fragments of *Brachythecium* and *Hypnum*. But at the western and southern edges of the forests, the moss mats nowadays often don't develop at all, or die off completely, and on these better-lit *Salix*-trees species-rich lichen vegetations can develop on primarily or secondarily bare bark.

Remarkably, so far *Hyperphyscia lucida* could only be traced in the extreme southwestern parts of the forests. These current patterns could be accidental starting points of colonization. Another explanation could be a preference of this member of a mainly tropical genus for mildly shaded habitats in combination with a tolerance for high temperatures. Tree trunks and low branches in this part of the forest – especially just beyond the forest edge – are somewhat shaded by the canopy, but the southern and western periphery of the forest floor here can get extremely heated by insolation. Keeping climate change in mind, it must be noted that in the Netherlands, with basically a temperate, suboceanic climate, and located at ca 52° northern latitude, for the first time in history, in 2019 a maximum temperature above 40°C was measured. The detrimental effects of summer exposure are probably attenuated by the shelter of a 2–3 m high uprising *Urtica*-vegetation.

In Table 1, the accompanying species of *H. lucida* are listed in order of presence, from relevés on 14 willow trees. The most constant companions are *Hyperphyscia adglutinata*, *Phaeophyscia orbicularis* (Neck.) Moberg, *Xanthoria parietina* (L.) Beltr. and *Hypnum cupressiforme*, all mostly ubiquitous species of neutral to basic, eutrophic bark. Among the frequent companions there are some very remarkable examples of a rapidly changing lichen flora in the Netherlands. Since long e.g. *Strigula taylori* (Carroll ex Nyl.) R.C. Harris was very rare in our country. In the Biesbosch it was first discovered in 2015 and in just a few years it has become one of the commonest microlichens on (rejuvenating) willow branches in the forests. *Porina byssophila* (Körb. ex Hepp) Zahlbr. has only been recorded in the Netherlands very recently (<www.verspreidingsatlas.nl/7539#>, first record in the Netherlands in the Biesbosch, leg. L. Sparrius 24-3-2019), but also this perithecioid lichen seems to increase 'explosively' in 2020, given its presence in 7 out of 14 relevés. After its first appearance in the Netherlands in 2015 the subtropical *Physciella chloantha* (Ach.) Essl. is now also rapidly expanding its range (<wwww.verspreidingsatlas.nl/7450>), also in the Biesbosch. *Strangospora deplanata* (Almq.) Clauzade & Cl. Roux was found in 2019 in the Biesbosch, new to the Netherlands (van der Kolk et al. 2019). It is has not yet turned up elsewhere in our country but surprisingly it was present in one relevé with *H. lucida*.

Hyperphyscia lucida not only acts as a pioneer, it has also been found overgrowing *H. adglutinata*, *Phaeophyscia orbicularis*, *Physcia adscendens* (Fr.) H. Olivier, *Xanthoria parietina* and (Fig. 14) *Hypnum cupressiforme*.

How can an undescribed macrolichen turn up in western Europe?

In the field I initially ignored the first, luxurious specimen of the new species as a 'whitish' *Hyperphyscia adglutinata* and went on, after all *Hyperphyscia* was a 'monotypic' genus in Europe. Only at the second tree the penny dropped and a search for a name began, which resulted in the description of *Hyperphyscia lucida*. But lichen species, and certainly macrolichens are not often described new for science from (western) Europe nowadays, so how could this new *Hyperphyscia* turn up in the Netherlands?

The species probably was not overlooked all this time. There is a long tradition of lichenology in Europe and most areas are well explored, certainly also the Netherlands and the Biesbosch. As for the Netherlands, its habitat, relatively old willow forest in a very fertile environment, probably did not exist until very recently (Tibell et al. 2019). Also, *Hyperphyscia lucida* is not some minute microlichen that can easily escape attention, and the differences with *H. adglutinata* are well defined and not very 'cryptic'.

Perhaps the new species is wrongly described? As for now the combination of aggregated, laminal pustules, a clear prothallus and diffuse, farinose to coarsely isidioid soralia seems however unique for the new *Hyperphyscia lucida* and

Figure 14. Luxurious, young thallus (17 mm across) of *Hyperphyscia lucida*, coll. v. d. Pluijm 3620. On the right side growing on bark of *Salix*, with appressed, broad lobes, on the left with loosely attached thallus lobes overgrowing the moss *Hypnum cupressiforme*, with groups of pustules and with diffuse, farinose to isidioid soralia.

is not documented in descriptions or pictures of currently described species. In the recent COVID-19 era, a review of herbarium specimens from outside the Netherlands has not yet been performed by me. Should the Dutch taxon nevertheless belong to an existing species, the concept of that species would then have to be widened considerably. And, if it were a species from maybe Argentina or Kenya, how could it end up here in semi-natural willow forests in western Europe?

A speculative explanation could be that *H. lucida* originated as a new species in the Biesbosch in situ. Could it be possible that the common *H. adglutinata* recently evolved into *H. lucida* here? Some parameters may have been favourable for this. Climate conditions have been exceptional in our country over the past decade, with very mild winters, and summers breaking drought and heat records. This could have resulted in a 'subtropical' selection filter over 'temperate' populations of *H. adglutinata*. Also, genetic diversity in local populations of *H. adglutinata* may have increased, given that nowadays in the Biesbosch thalli of this species are often provided with apothecia and pycnidia. Of course, such hypotheses can only be tested with DNA-techniques. But there are examples of such events being real. The recently described moss *Leptodon corsicus* Enroth, A. Sotiaux, D. Quandt & Vanderp. differs morphologically strikingly from other species of the genus. Yet, phylogenetic analysis of chloroplast and nuclear DNA sequences shows that *L. corsicus* is deeply nested within *L. smithii* (Hedw.) F. Weber & D. Mohr (Sotiaux et al. 2009). They suggest that in a recent speciation process minor changes in the DNA (a few mutations, or changes in gene expression) of *L. smithii*, might have caused tremendous phenotypic changes, resulting in *L. corsicus*. Hypothetically this could also apply to *H. lucida* and is worth testing.

Conclusion

This study of a local population of a new species *Hyperphyscia lucida* has shown that e.g. thallus colour, lobe and soralia morphology can vary considerably, as developmental stages or as a result of varying ecological factors. Many more species of the genus *Hyperphyscia* show phenotypical plasticity, which complicates the taxonomy of the genus. Also, species concepts are sometimes almost solely based on a single character. Thus, according to Scutari (1997) three pairs of species in *Hyperphyscia* only differ by having 1- or 3-septate spores. And in Filippini et al. (2015), regarding one of those species pairs, *Hyperphyscia cochlearis* has now been synonymised with *H. variabilis*. A global revision of *Hyperphyscia* is certainly in need, preferably from an integrative approach that also uses DNA-techniques. For this genus DNA-data are still scarce. In GenBank, (<www.ncbi.nlm.nih.gov/nuccore/?term=Hyperphyscia>, accessed 20 June 2020) so far 19 nucleotide samples of only three species (*Hyperphyscia adglutinata*, *H. confusa* and *H. crocata* Kashiw.) out of 23 species are deposited.

In recent decades semi-natural willow forests in the Netherlands have proven to be regional hotspots for lichens. With the aging of these woodlands – the maximum age of trees can be 80–90 years now – lichen diversity is still increasing, and many locally rare and even some 'old-woodland' species have now established themselves, e.g. *Chaenotheca* spp., *Coniocarpon cinnabarinum* DC., *Phaeographis dendritica* (Ach.) Müll. Arg., *P. smithii* (Leight.) de Lesd. and *Sporodophoron cretaceum* (Hue) Ertz & Frisch (van der Pluijm and van Dort 2016), and in 2019 *Chaenotheca biesboschii* Tibell & van der Pluijm was described from here (Tibell et al. 2019). The new *Hyperphyscia lucida* also adds to this trend. Monitoring these developments is very interesting, especially since there are few or no comparable examples from the past of such 'old' willow forests in an extremely fertile environment in western European lowlands. In these urbanized regions e.g. recreation, pollution and land development remain a constant threat and these forests deserve a high conservation status.

Selected specimens examined

Hyperphyscia lucida

– the Netherlands, prov. N-Br., Biesbosch, Middelste Jannezand, GPS 51.7306N, 4.8483E; 2 m high on vertical, 50-year old Salix-stem in freshwater tidal willow forest, 'tree 5'; 5-3-2020, leg. van der Pluijm 3641a (Holotype, L).

– Idem, leg. van der Pluijm 3641b (Isotype, L).
– Idem, leg. van der Pluijm 3641c (Isotype, L).
– the Netherlands, prov. N-Br., Biesbosch, Middelste Jannezand, GPS 51.7300N, 4.8482E; 0.5–2 m high on vertical, young branch in 50-year old *Salix* forest in freshwater tidal area. Tree '1', with *Physciella chloantha*, *Strangospora deplanata*, *Orthotrichum obtusifolium*; 27-3-2020, leg. A. van der Pluijm 3650a and 3650b (L, Herb. van der Pluijm).
– the Netherlands, prov. N-Br., Biesbosch, Middelste Jannezand, GPS 51.730N, 4.8482E; 1–1.9 m high on vertical, ca 60-year-old willow stem, 60 cm diam., in freshwater tidal willow forest, tree '2', partly growing over mosses, with *Hyperphyscia adglutinata* c. apoth. (coll. v. d. Pluijm 3634) and (outside relevé) *Ramalina lacera*; 7-2-2020, leg. A. van der Pluijm 3620 (L, Herb. van der Pluijm).

Hyperphyscia adglutinata

– the Netherlands, prov. N-Br., Biesbosch, Middelste Jannezand, GPS 51.730N, 4.8482E; 1.5 m high on vertical, ca 60-year-old willow stem, 60 cm diam., in freshwater tidal willow forest, tree '2', with *Hyperphyscia lucida* and (outside relevé) *Ramalina lacera*; with apothecia and pycnidia; 7-2-2020, leg. A. van der Pluijm 3634 (Herb. van der Pluijm).
– the Netherlands, prov. N-Br., Biesbosch, Benedenste Jannezand, GPS 51.731N, 4.843E; extensively, 1–4 m high on sun exposed willow stem, western border tidal willow forest; with pycnidia; 27-3-2020, leg. A. van der Pluijm 3647 (Herb. van der Pluijm).

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