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Morphological evidence for the distinction of *Alyxoria lichenoides* and *A. viridipruinosa* from *A. varia*

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Abstract. The epiphytic lichen *Alyxoria varia* is often interpreted as an extremely variable species or as a complex of multiple species that is not yet well understood. *Alyxoria lichenoides* is sometimes recognized as a separate species, and recently *Alyxoria viridipruinosa* was newly described. However, it is still poorly known which characteristics are useful to distinguish these species from *A. varia*. Here, we studied and measured morphological characteristics of 83 specimens of *A. varia* s.l., mainly from the Netherlands, but with some additional specimens from other European countries. We measured the dimensions of the lirellae, ascospores and conidia. We found that *Alyxoria lichenoides*, *A. varia* and *A. viridipruinosa* can be reliably separated by differences in the size of their conidia. There are also differences in the size of the lirellae, size of the pycnidia and ascospores, but due to overlap not all specimens can be identified based on those characteristics alone. *Alyxoria lichenoides* and *A. viridipruinosa* are very variable species with respect to the abundance of pycnidia, size and shape of the lirellae, thallus color and pruina presence. Some morphotypes can, however, still be identified with certainty in the field. *Alyxoria lichenoides* is currently one of the most common epiphytic lichens in the Netherlands, especially in coastal areas. It occurs in woodlands, parks and on roadside trees. *Alyxoria viridipruinosa* occurs in similar habitats, but is somewhat scarcer, and due to its smaller size and generally inconspicuous thallus easily overlooked. *Alyxoria varia* is rare in the Netherlands and occurs in drier habitats. It prefers woodlands and parks and is not bound to coastal areas. We recommend that lichenologists in Europe distinguish *Alyxoria varia*, *A. viridipruinosa* and *A. lichenoides* as three separate species. Future studies that include molecular data could reveal whether even more species are involved.

Key words: *Arthoniales*, *Ascomycetes*, biodiversity, epiphyte, lichens, *Opegraphaceae*, species delimitation, taxonomy

Introduction

Alyxoria varia (Pers.) Ertz & Tehler is a widespread corticolous lichen with lirellate apothecia (Wirth et al. 2013; Wieczorek 2018; Cannon et al. 2021). The species was first described more than 200 years ago as *Opegrapha varia* Pers. (Persoon 1794). Recent molecular studies showed that *Alyxoria varia* belonged to a group that is distinct from *Opegrapha* Ach. (Ertz et al. 2009), and shortly after the genus *Alyxoria* Ach. ex Gray was resurrected to accommodate *Alyxoria varia* (Ertz & Tehler 2011).

Throughout time numerous species have been described that are now considered to be synonyms of *Alyxoria varia*. Authors in the 20th century often distinguished *Opegrapha lichenoides* Pers., *Opegrapha pulicaris* Röhl., *Opegrapha diaphora* Ach. and *Opegrapha rimalis* Ach. as four separate species (e.g., Erichsen 1957; Poelt 1969). All of these species are now, however, commonly treated as synonyms of *Alyxoria varia*, since no consistent differences were known that justify the separation into multiple species (e.g., Wieczorek 2018). Consequently, *Alyxoria varia* is therefore currently most commonly interpreted as an extremely variable species or a complex of species which is not yet well understood (Wieczorek 2018; Cannon et al. 2021).

Of all the species that are considered as synonyms, *Alyxoria lichenoides* (Pers.) Cl. Roux is a taxon that is sometimes still recognized as a separate species (Pentecost & Coppins 1983; Roux et al. 2025). *Alyxoria lichenoides* was described to differ from *Alyxoria varia* by its shorter and broader, ellipsoid or rounded apothecia (vs. longer and relatively narrow and elongated apothecia in *Alyxoria varia*) (Persoon 1794; Erichsen 1957; Poelt 1969). Recently, a third species was described from England, namely *Alyxoria viridipruinosa* (Coppins & Yahr) Ertz (Lumbsch et al. 2011). This species was

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described to differ from *Alyxoria varia* by its smaller lirellae, smaller ascospores, smaller pycnidia and shorter conidia. It was then also reported from the Netherlands (Timmerman & Aptroot 2012) and Germany (Schiefelbein et al. 2014). In its original description, however, *Alyxoria viridipruinosa* was not compared to *Alyxoria lichenoides*. In France, both *Alyxoria lichenoides* and *Alyxoria viridipruinosa* are treated as separate species from *Alyxoria varia* (Toussaint et al. 2021; Roux et al. 2025). Roux et al. (2025) discussed the morphological differences between *Alyxoria viridipruinosa* and *Alyxoria lichenoides*, and suggested that conidia size is a diagnostic feature separating *Alyxoria lichenoides* from *Alyxoria viridipruinosa*, but that the sizes of the apothecia and ascospores show overlap between the species.

In the Netherlands, we observed a large morphological variation in lichens that were reported as *Alyxoria varia* or *Alyxoria viridipruinosa*. Most specimens, however, showed characteristics intermediate between the descriptions of those two species, which we suspected could be explained by the presence of *Alyxoria lichenoides*. We found that, as pointed out by Roux et al. (2025), it was possible to reliably separate our specimens into three species based on conidia size, and that these three species match the concepts of *Alyxoria varia*, *A. lichenoides* and *A. viridipruinosa*. In order to document the morphological variation in these species and determine which characteristics are useful for their identification, we collected and studied a large number of specimens and performed measurements on the sizes of apothecia, ascospores and conidia. Here, we report on the variation and usefulness of morphological characteristics for the separation of *Alyxoria varia*, *A. lichenoides* and *A. viridipruinosa*. Furthermore, we provide complete updated descriptions and illustrations of the three species and discuss their distribution and ecology.

Material and methods

Material collection

Specimens of corticolous *Alyxoria varia*, *A. lichenoides* and *A. viridipruinosa* were collected, dried and stored in the private herbaria of the authors. Most specimens were collected in the Netherlands, supplemented by a few specimens that were collected in other European countries. Additionally, specimens were borrowed from other Dutch and French lichenologists. In the herbarium of Naturalis Biodiversity Center (L), we studied the lectotype of *Alyxoria varia*, the lectotype of *Opegrapha chlorina* Pers., and the lectotype and a residual syntype of *A. lichenoides*. In total, measurements were performed on 83 specimens (47 of *Alyxoria lichenoides*, 22 of *A. varia* and 14 of *A. viridipruinosa*). We have seen and studied many other specimens in the Netherlands (hundreds of additional specimens of *Alyxoria lichenoides* and dozens of specimens of *Alyxoria viridipruinosa*), but due to time constraints those were not measured in detail if they resembled a morphotype that was already measured in detail before.

Morphological examination

Specimens were studied with a dissecting microscope (7–45× magnification) and light microscope (40–1000× magnification). Microscopic slides were mounted and measurements performed in water, unless stated otherwise. Standardized measurements were performed based on images. Images were captured with a camera mounted on a third ocular on the dissecting microscope (for macroscopic images to measure apothecia) or light microscope (for microscopic images, at 400× magnification for ascospores and at 1000× magnification for conidia), or with an extended tube directly via a ×4 microscope lens (for additional macroscopic images). Using a photoshop program, the length and width of apothecia, ascospores and conidia was measured in pixels, and then converted to micrometres.

We aimed to measure 10 apothecia, 30 conidia and as many as possible ascospores per specimen. In total, we measured the length and width of a total of 2,005 conidia in 64 specimens (1,121 conidia of *Alyxoria lichenoides*, 434 of *A. varia* and 450 of *A. viridipruinosa*), the number of septa, length and width of a total of 904 ascospores in 51 specimens (508 ascospores of *Alyxoria lichenoides*, 313 of *A. varia* and 83 of *A. viridipruinosa*; length and width were measured excluding the perispore; ascospores were often scarce in specimens of *A. viridipruinosa*) and the length and width of in total 795 apothecia in 80 specimens (460 apothecia of *Alyxoria lichenoides*, 215 of *A. varia* and 120 of *A. viridipruinosa*). Due to time constraints, not all characteristics were measured from each specimen. Dimensions of conidia, ascospores and lirellae are reported as 5^{th}–95^{th} percentiles.

Results

Conidia dimensions

The dimensions of conidia revealed a clear grouping among the specimens that matched the species concepts of *Alyxoria lichenoides*, *Alyxoria varia* and *Alyxoria viridipruinosa* (Fig. 1). Specimens of *Alyxoria viridipruinosa* had the shortest conidia, measuring 3.0–3.7 × 1.0–1.4(–1.5) µm. The conidia were most often bacilliform, narrow (1.0–1.2 µm broad) and sometimes slightly curved. However, sometimes slightly broader (up to about 1.5 µm broad) more ellipsoidal conidia were observed. These variations in shape were often observed within the same specimen, and may be interpreted as two types of conidia. Specimens of *Alyxoria varia* contained two types of conidia, broader conidia measuring 3.7–4.8 × 1.6–2.1 µm and narrow conidia measuring 3.3–4.5 × 0.9–1.3 µm. Conidia of the broad type were always observed when pycnidia were present. Conidia of the narrow type were observed in the same specimens and often seemingly within the same pycnidium. All specimens of *Alyxoria lichenoides* contained one type of bacilliform conidia measuring 4.0–5.3 × 1.2–1.6 µm, intermediate between the broad and narrow types of conidia of *Alyxoria varia*.

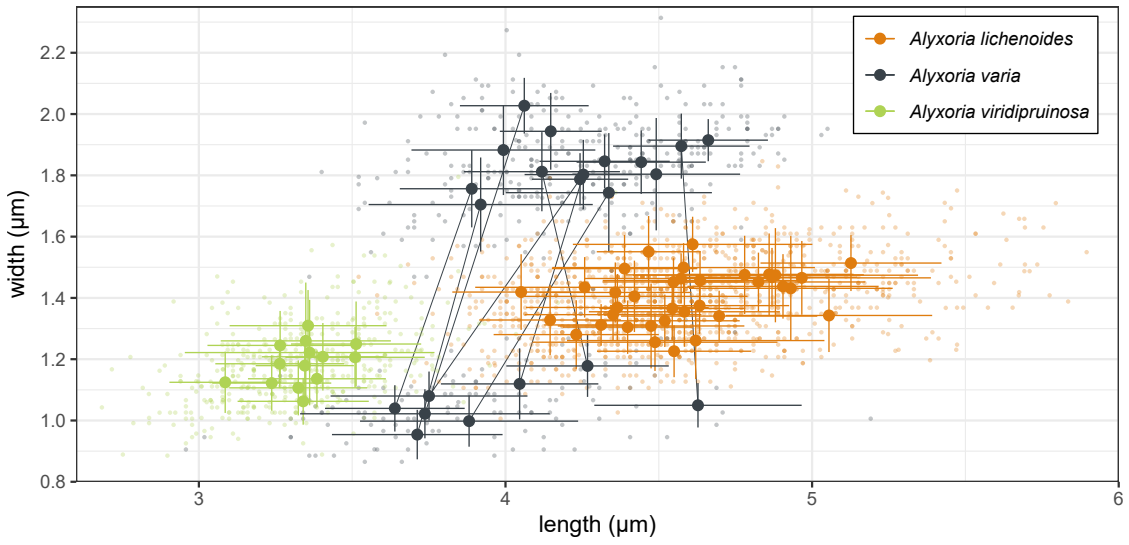

Figure 1. Mean length and width of conidia (±SD) of specimens of *Alyxoria lichenoides*, *A. varia* and *A. viridipruinosa*. From most specimens 30 conidia were measured. For *Alyxoria varia*, the two types of conidia measured in the same specimen are connected with a thin line. Small dots in the background are measurements of individual conidia.

Apothecia dimensions

The dimensions of the apothecia differed between the three species, but there was some overlap (Fig. 2). The apothecia of *Alyxoria viridipruinosa* were the smallest and narrowest of the three species, measuring 0.20–0.55 × 0.08–0.23 mm. The apothecia tend to be more often closed and with a less exposed disc compared to the other two species. The apothecia of *Alyxoria lichenoides* were very variable, measuring 0.35–0.85(–1.2) × 0.15–0.40 mm. Typically the apothecia were elliptical or ovoid and broad, but sometimes more elongated and then they were sometimes also once-branched. The disc was often widely exposed. The apothecia of *Alyxoria varia* were on average the largest among the studied species, measuring 0.5–1.3(–1.5) × 0.15–0.3 mm. The apothecia in *A. varia* were relatively narrow, but usually still with a widely exposed disc.

The size of the apothecia in the lectotype and in a residual syntype of *Alyxoria lichenoides* fell within the range of other specimens of *A. lichenoides* measured, but outside the range of *A. varia* and *A. viridipruinosa*. The size of the apothecia in the lectotypes of *Alyxoria varia* and *Opegrapha chlorina* fell within the range of other specimens of *A. varia* measured, but outside the range of *A. lichenoides* and *A. viridipruinosa*.

Ascospore characteristics

Ascospore characteristics differed between the three species, but there was considerable overlap between *Alyxoria viridipruinosa* and *A. lichenoides* and between *A. lichenoides* and *A. varia* (Figs 3, 4). Measurements of ascospores were taken excluding the perispore, which was present in all species and approximately 1 µm wide.

On average, the ascospores of *Alyxoria viridipruinosa* were the smallest of the three species, measuring 13.7–20.6 × 3.5–5.4 µm, and had the lowest number of septa, being predominantly 3–4 septate (Fig. 4A–C). The ascospores of *Alyxoria lichenoides* were intermediate in

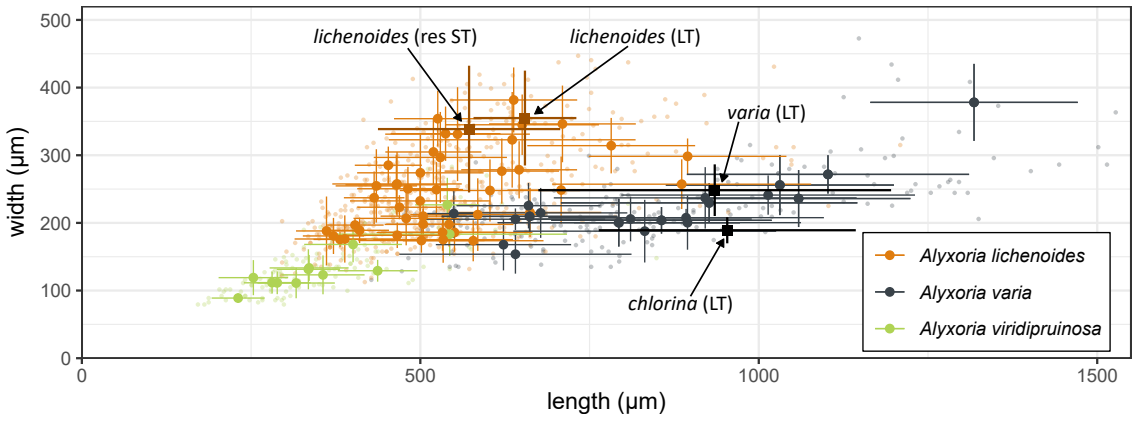

Figure 2. Mean length and width of apothecia (±SD) of specimens of *Alyxoria lichenoides*, *A. varia* and *A. viridipruinosa*. Small dots in the background show measurements of individual apothecia. Additional dots are shown for the lectotype of *Alyxoria lichenoides* ("*lichenoides* LT"), a residual syntype of *A. lichenoides* ("*lichenoides* res ST"), the lectotype of *Alyxoria varia* ("*varia* LT") and the lectotype of *Opegrapha chlorina* ("*chlorina* LT").

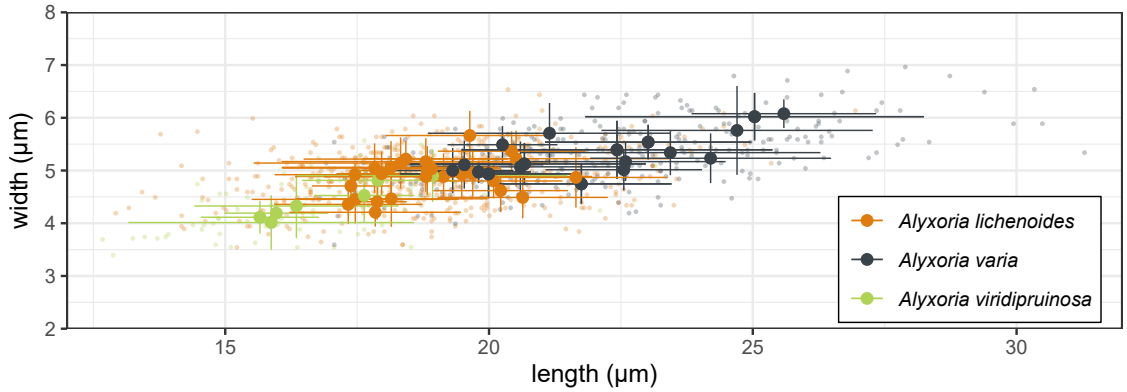

Figure 3. Mean length and width of ascospores (±SD) in specimens of *Alyxoria lichenoides*, *A. varia* and *A. viridipruinosa*. Small dots in the background show measurements of individual ascospores.

size, measuring 15.5–22.6 × 4.0–5.7 µm, and were predominantly 4–5 septate (Fig. 4D–F). The ascospores of *Alyxoria varia* were the largest of the three species, measuring 18.1–26.7 × 4.5–6.3 µm, and were predominantly 5–6 septate (Fig. 4G–I).

Discussion

Our measurements confirm the observations made by Roux et al. (2025), namely that the dimensions of the conidia are a consistent and diagnostic characteristic to separate *Alyxoria lichenoides*, *A. varia* and *A. viridipruinosa* (Fig. 5). Pycnidia are in all three species almost always present (although sometimes scarce and inconspicuous when lirellae are abundant), thus most specimens can be identified with certainty by measuring the conidia. However, since the size differences between the species is small, accurate measurements should be taken at a 1000× magnification.

Other morphological characteristics are to a certain extent also useful to separate the three species (Table 1). Macroscopically, especially *Alyxoria lichenoides* and *A. viridipruinosa* show considerable variation in appearance. The presence, size and shape of apothecia, and presence and abundance of pycnidia vary strongly between specimens, even under seemingly similar conditions. Still, the size and shape of apothecia in combination with the size of the pycnidia can in many instances be used in the field to correctly identify the species. Specimens with large, elongated and epruinose apothecia and seemingly

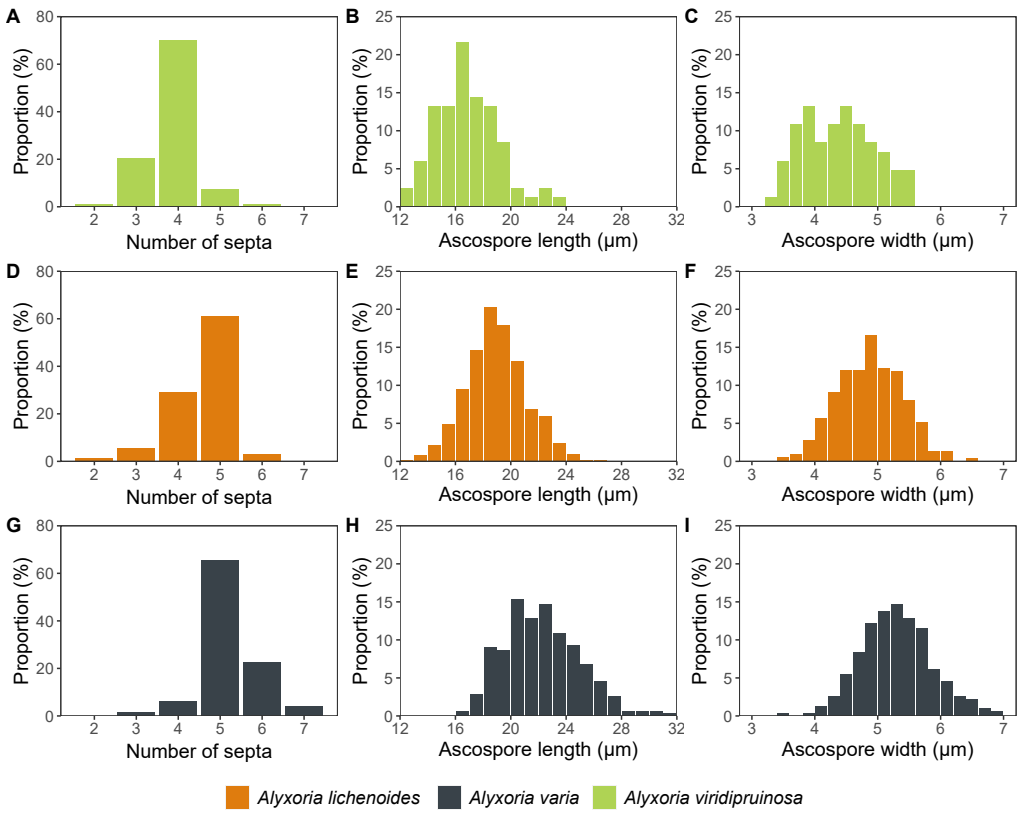

Figure 4. Ascospore characteristics. A–C – distribution of the number of septa (A), ascospore length (B) and ascospore width (C) in *Alyxoria viridipruinosa*; D–F – distribution of the number of septa (D), ascospore length (E) and ascospore width (F) in *Alyxoria lichenoides*; G–I – distribution of the number of septa (G), ascospore length (H) and ascospore width (I) in *Alyxoria varia*.

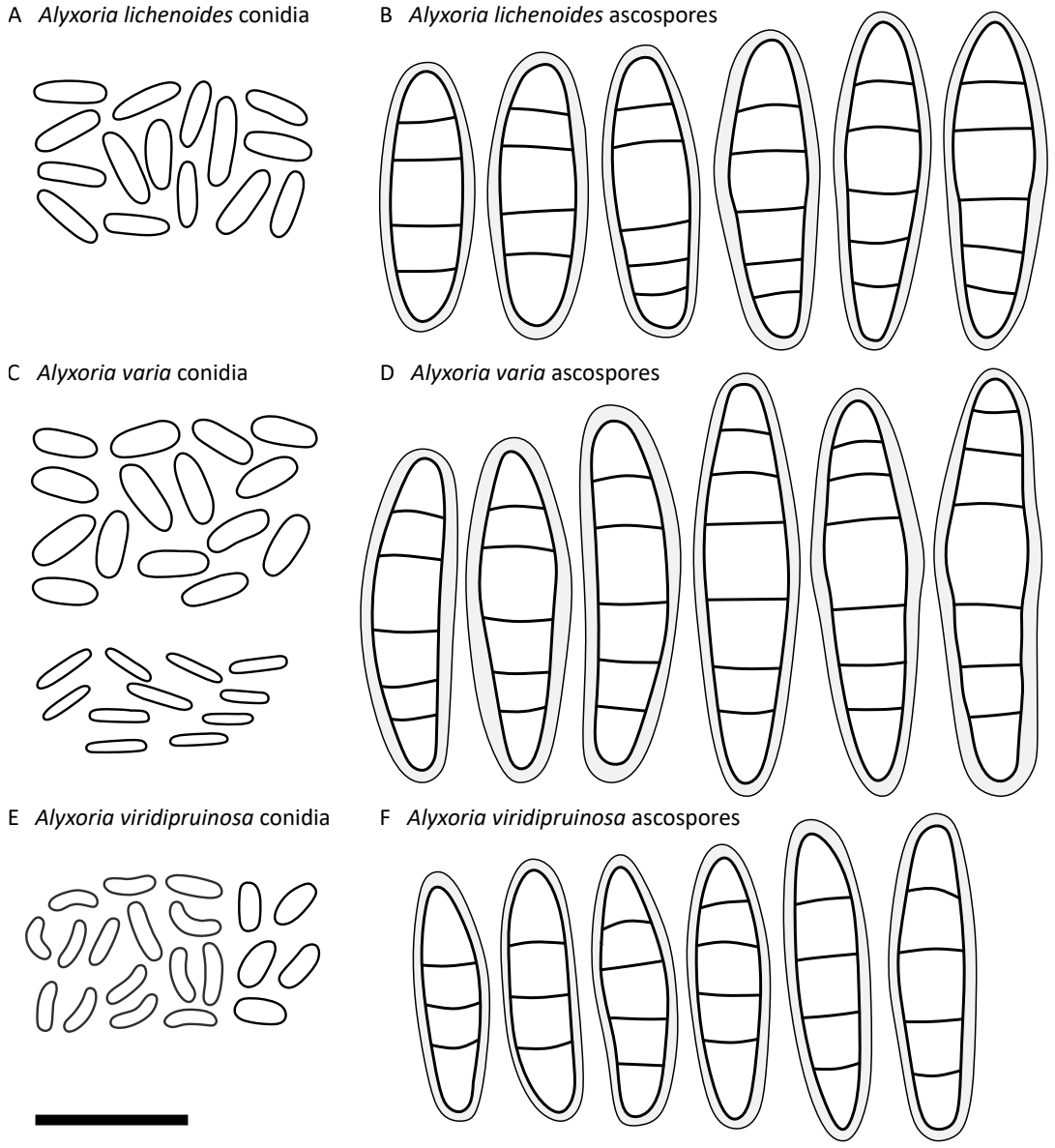

Figure 5. A, B – conidia (A) and ascospores (B) of *Alyxoria lichenoides*; C, D – conidia (C) and ascospores (D) of *Alyxoria varia*; E, F – conidia (E) and ascospores (F) of *Alyxoria viridipruinosa*. Scale = 10 µm.

Table 1. Key morphological characteristics to distinguish the species examined in this study.

	Alyxoria viridipruinosa	*Alyxoria lichenoides*	*Alyxoria varia*
Lirellae	Narrowly ellipsoid, elongate, stellate. Disc not or slightly exposed. 0.20–0.55 × 0.08–0.23 mm	Ellipsoid, rounded, triangular. Disc widely exposed. 0.35–0.85(–1.2) × 0.15–0.40 mm	Elongate, narrowly ellipsoid, linear. Disc narrowly to widely exposed. 0.5–1.3(–1.5) × 0.15–0.3 mm
Ascospores	(2–)3–4(–6) septate 13.7–20.6 × 3.5–5.4 µm	(2–)4–5(–6) septate 15.5–22.6 × 4.0–5.7 µm	(3–)5–6(–7) septate 18.1–26.7 × 4.5–6.3 µm
Pycnidia	(20–)40–110(–160) µm	(70–)100–180(–210) µm	70–130 µm
Conidia	3.0–3.7 × 1.0–1.4(–1.5) µm	4.0–5.3 × 1.2–1.6 µm	Two types: 3.7–4.8 × 1.6–2.1 µm 3.3–4.5 × 0.9–1.3 µm

no or few pycnidia belong to *A. varia* (note that confusion is possible with other *Alyxoria* species, notably *Alyxoria culmigena* (Lib.) Ertz and *Alyxoria ochrocheila* (Nyl.) Ertz & Tehler, that have 3-septate ascospores). Specimens with medium-sized, broad apothecia and large pycnidia belong to *A. lichenoides*. Specimens with small, narrow apothecia and small pycnidia belong to *A. viridipruinosa*. Furthermore, *Alyxoria lichenoides* usually forms a conspicuous, often cracked and grey-white thallus, whereas in *A. viridipruinosa* the thallus is generally thinner or evanescent. *Alyxoria varia* forms a conspicuous thallus which is whitish or greyish. Green-yellow pruina can be present on the thallus and apothecia in both *Alyxoria lichenoides* and *A. viridipruinosa*, and is not a useful characteristic

to separate those species. With experience, many typical morphotypes can be identified with certainty in the field (also see notes under the species), but for intermediate morphs the size of the conidia should be measured to confirm the identification.

The ascospores also differ between the three species, but since there is considerable overlap we do not recommend identifying a specimen based on the ascospores without considering other characteristics. Ascospore dimensions were repeatedly reported as a useful feature to separate *Alyxoria viridipruinosa* from *A. varia* (Lumbsch et al. 2011; Timmerman & Aptroot 2012; Cannon et al. 2021). However, none of these comparisons accounted for the existence of *Alyxoria lichenoides*, which has ascospores that are intermediate between those of *Alyxoria viridipruinosa* and *A. varia*. In our observations, *Alyxoria varia* has narrower and also slightly shorter ascospores than previously described (Smith et al. 2009; Wirth et al. 2013; Cannon et al. 2020). The large ascospore size range for *Alyxoria varia* given by Wieczorek (2018) is likely based on specimens of *Alyxoria lichenoides* and *Alyxoria varia* combined, and matches our measurements of those species.

Besides morphological differences there also seem to be differences in ecology between the three species. In the Netherlands, *Alyxoria varia* is a rare species, usually found in relatively dry habitats in older parks and woodlands, for example on old *Fagus sylvatica* trees in open forests or *Carpinus betulus* trees in old hedges. Additional specimens of *Alyxoria varia* found by the authors (not measured in detail for this study) in Southern Sweden and the mountains of Central Europe were usually made on the base of old *Quercus* and *Fraxinus*, also in fairly dry conditions. Near the Mediterranean, it was also collected on bark of *Quercus ilex* in open forest. In Central and Northern Europe, *Alyxoria varia* seems to be the most common of the three species.

On the other hand, *Alyxoria lichenoides* and *A. viridipruinosa* both seem to prefer more coastal, Atlantic conditions, and softer, basic bark. Both species are in the Netherlands most commonly found on the trunks of *Salix*, *Populus*, *Quercus* and *Sambucus* trees. In the Netherlands, especially *Alyxoria lichenoides* occurs commonly in young forests with a high humidity, as well as on the north side of wayside trees near the coast. The abundance of *Alyxoria lichenoides* has spectacularly increased over the last decades, and currently it is one of the dominant epiphytic lichen species on roadside trees in the coastal provinces. For example, it was recently recorded at 295 out of 451 monitoring sites in Zuid-Holland (as *Alyxoria varia* in Verboom et al. 2025) and at 261 out of 283 monitoring sites in Zeeland (as *Alyxoria varia* in van der Kolk et al. 2025). *Alyxoria viridipruinosa* is sometimes found together with *A. lichenoides*, but seems to prefer slightly more sheltered conditions. In mixed species woodlands on the Dutch Wadden Islands, for example, *Alyxoria viridipruinosa* is relatively common on sheltered oak trees, whereas *Alyxoria lichenoides* is currently rare in this habitat. *Alyxoria viridipruinosa* is clearly rarer in the Netherlands than *Alyxoria lichenoides*, but locally the species can occur frequently. Due to the inconspicuous thallus, it is also more easily overlooked.

Many other corticolous *Alyxoria* species are known in Europe that can be confused with the species treated here. *Alyxoria ochrocheila* and *Alyxoria culmigena* can be distinguished from the species treated here by the 3-septate ascospores. *Alyxoria xerica* (Torrente & Egea) Haluwyn & Cl. Roux is characterized by the olivaceous, K+ greenish epithecium. The latter species is not known from the Netherlands and therefore not included in this study.

The shape and dimensions of the apothecia of the species concepts of *Alyxoria lichenoides* and *Alyxoria varia* presented here match with their respective lectotypes. Unfortunately, the lectotype material of *Alyxoria lichenoides* is infested with a lichenicolous fungus and we could not find conidia. The shape and dimensions of the apothecia of the lectotype of *Opegrapha chlorina* (Persoon 1810) matches those of *Alyxoria varia* specimens. Therefore, even though the presence of green pruina is atypical for *Alyxoria varia*, we consider *Opegrapha chlorina* a synonym of *Alyxoria varia*. More importantly, the name *Opegrapha chlorina* should not be applied for green morphotypes of *Alyxoria lichenoides* (Erichsen 1957).

In conclusion, our study shows that *Alyxoria lichenoides*, *Alyxoria varia* and *Alyxoria viridipruinosa* are three morphologically distinct taxa that can be separated by their conidia size, as well as a combination of other characteristics. *Alyxoria lichenoides* was previously often included in the species concept of *Alyxoria varia*, but is a separate species that is probably common along the Atlantic coast of Europe. The existence of *Alyxoria lichenoides* explains previous inconsistencies in the reported morphological differences between *A. varia* and *A. viridipruinosa*, that often at least partially included specimens of *A. lichenoides* for one of those two species. We recommend that lichenologists in Europe consistently separate *Alyxoria lichenoides* and *A. viridipruinosa* from *A. varia*. Future studies can attempt to include molecular data to study whether even more species are involved.

Taxonomy

Alyxoria lichenoides (Pers.) Cl. Roux, Catalogue des Lichens et Champignons Lichénicoles de France Métropolitaine, 2e édition revue et augmentée 1: 1126. 2017. (Fig. 6)

MycoBank MB 820258

≡ *Opegrapha lichenoides* Pers., Ann. Bot. (Usteri) 7: 30. 1794.

Type: Europe, France, hab. ad ligna salicis, C.H. Persoon (L-L0056731 – lectotype!); Europe, C.H. Persoon (L-L0056732 – residual syntype!).

=*Lichen nothus* Ach., Lich. suec. prodr. (Linköping): 19. 1799. ≡ *Opegrapha notha* (Ach.) Ach., Methodus, Sectio prior (Stockholmiæ): 17. 1803. ≡*Alyxoria notha* (Ach.) Gray, Nat. Arr. Brit. Pl. (London) 1: 504. 1821. ≡*Scaphis notha* (Ach.) Eschw., Syst. Lich.: 25. 1824. ≡*Graphis notha* (Ach.) Trevis., in Rabenhorst, Hedwigia 10(10): 155. 1871.

Description. Thallus thin, smooth or cracked, white, white-grey or brown-grey, epruinose or sometimes green-yellow pruinose. Photobiont trentepohlioid.

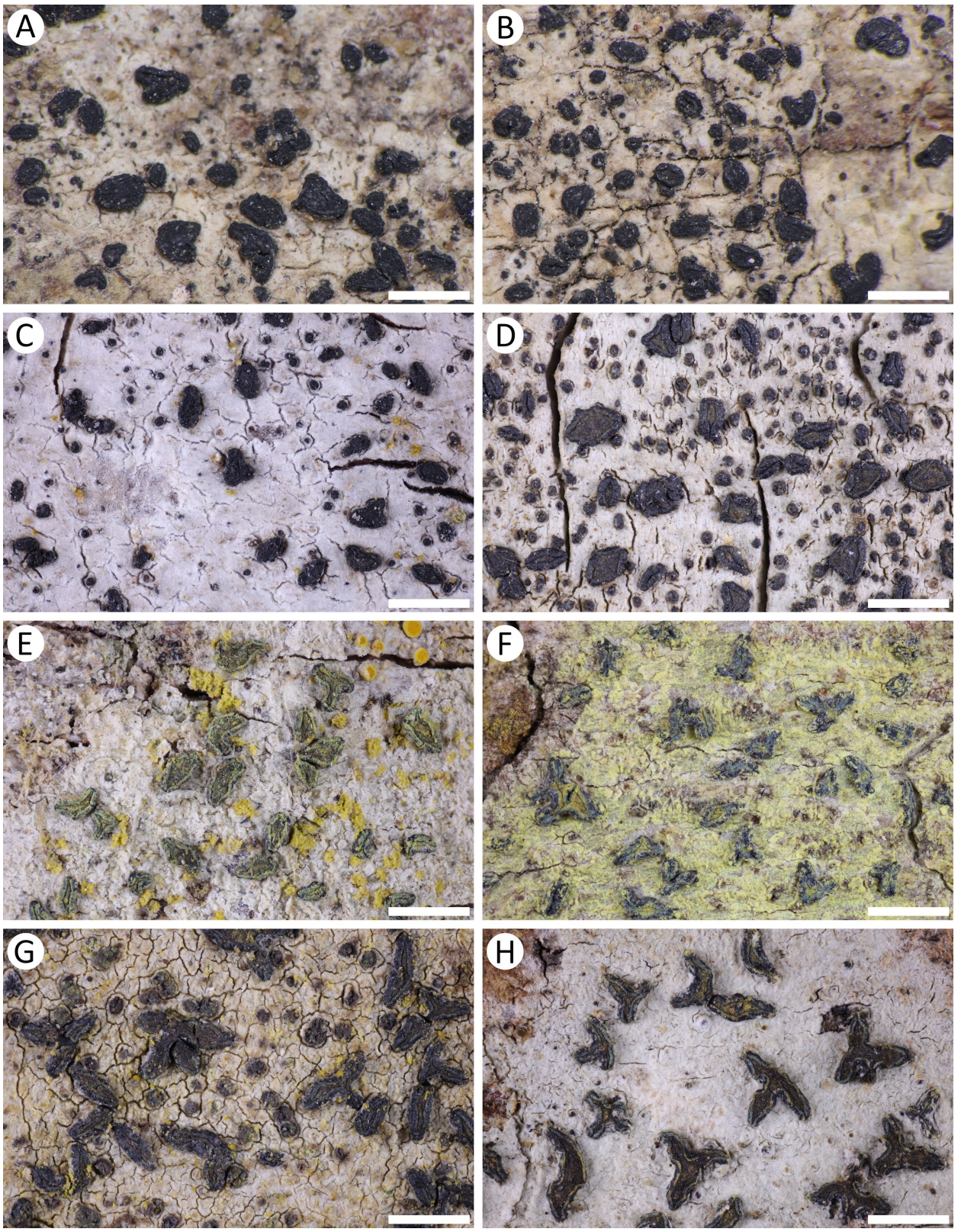

Figure 6. *Alyxoria lichenoides*. A – lectotype (L0056731); B – residual syntype (L0056732); C – van der Kolk 3795; D – van der Kolk 3125; E – van der Kolk 2921; F – van der Kolk 3558; G – van der Kolk 3344; H – van der Kolk 1659. Scales: A–H = 1 mm.

Apothecia frequently present, scattered or sometimes contiguous, sessile, lirellate, 0.35–0.85(–1.2) × 0.15–0.40 mm, ellipsoid, rounded, triangular, sometimes linear or stellate, unbranched or once-branched, exciple margins raised above the disc, with a widely exposed disc, black, epruinose or yellow-green pruinose, sometimes orange pruinose or grey pruinose. Exciple brown-black in section, K–; hypothecium brown-black, K–; hymenium 60–90 µm, I+ red; epithecium brown, K– (but green-yellow pruina, when present, faintly K+ yellow). Paraphyses abundant, hyaline, branched. Asci fissitunicate, 45–65 × 11–18 µm, 8-spored. Ascospores 15.5–22.6 × 4.0–5.7 µm, (2–)4–5(–6) septate, narrowly ellipsoidal or somewhat clavate, the middle cell somewhat enlarged, with rounded ends;

perispore of ~1 µm, becoming brownish and wrinkled with age. Pycnidia usually present, abundant or sometimes scarce, (70–)100–180(–210) µm, black, epruinose or thinly white- or greenish-pruinose. Conidia bacilliform, hyaline, aseptate, straight, 4.0–5.3 × 1.2–1.6 µm.

Distribution in Europe. Confirmed from the Netherlands, Belgium, France, Great Britain and Spain (Aragón et al. 2025). Probably widespread along the Atlantic coast, but the precise distribution is currently unclear due to confusion with *Alyxoria varia*.

Ecology and habitat. In the Netherlands found in a wide range of habitats. Abundant on the trunks of roadside trees, as well as trees in woodlands and parks. Most abundant on *Fraxinus*, *Populus*, *Quercus*, *Salix* and *Sambucus*. Sometimes on dry lignum in sheltered situations, occasionally on north-facing walls. More common in coastal areas.

Notes. The color and thickness of the thallus, and the shape, size and color of the apothecia are very variable in this species. Nevertheless, typical morphs are recognizable in the field due to the combination of a fairly thick thallus, abundant and large pycnidia and broad apothecia (Fig. 6C, D). The size of the pycnidia is a useful field characteristic, especially when *Alyxoria lichenoides* grows intermixed with *Alyxoria viridipruinosa*. In *Alyxoria lichenoides* the pycnidia are often much larger [(70–)100–180(–210) µm] then those of *A. viridipruinosa* [(20–)40–110(–160) µm]. Morphotypes with thinner thallus, inconspicuous pycnidia (because they are scarce or covered by pruina) and somewhat narrower apothecia (Fig. 6E, F) can easily be confused with *Alyxoria viridipruinosa*, and we recommend to always confirm the identity of those morphs by measuring the conidia. Rarely *Alyxoria lichenoides* forms large and more elongated apothecia (Fig. 6G, H) that resemble those of *Alyxoria varia*, but also differ from those in the sizes of their conidia. Future molecular studies could investigate whether these morphs belong to a different or undescribed species not considered here.

Many previous records of both *Alyxoria varia* and *Alyxoria viridipruinosa* belong to this species. For example, the picture of *Alyxoria viridipruinosa* on the cover of Cannon et al. (2021), and the pictures of *Alyxoria varia* in Timmerman & Aptroot (2012) belong to *Alyxoria lichenoides*.

Over time many morphotypes and varieties have been described based on the presence or absence of pruina. Roux et al. (2025) distinguish morphotypes *lichenoides* (without pruina), *chlorina* (with yellow-green pruina on apothecia and sometimes also on thallus) and *nigrocaesia* (with blue-grey pruina on apothecia). The presence of yellow-green pruina almost certainly has no taxonomic value, since we frequently observed thallus parts and apothecia with and without yellow-green pruina within the same specimen. The lectotype of *Opegrapha chlorina* has apothecia resembling *Alyxoria varia* and not *Alyxoria lichenoides*, and thus the name *Opegrapha chlorina* should be considered a synonym of *Alyxoria varia*. We did not observe any specimens with blue-grey pruina.

Specimens examined. FRANCE. Finistère, Plouhinec, Guenvez, 3 Aug. 2020, on branches of cypres, Colibry 2960 2185; Pluguffan, 27 Nov. 2021, on *Platanus hybridus*, Rémy Ragot s.n. Nord, Bailleul, Conservatoire Botanique National, Jardin des plantes médicinales, 13 Mar. 2019, on *Liriodendron tulipifera*, Benoît Toussaint. Pas-de-Calais, Camiers, La Maison Dans la Dune, 20 Apr. 2021, on *Fraxinus excelsior*, Benoît Toussaint. Somme, Mers-les-Bains, Bois de Rompval, 22 Feb. 2022, on *Carpinus betulus*, Marine Cocquempot (herb. Van Haluwyn 183). NETHERLANDS. Gelderland, Afferden, Laarstraat, 51.87592°N, 5.63871°E, 8 Apr. 2022, on *Populus*, H. van der Kolk (herb. van der Kolk 2949); Blauwe Kamer, 51.9448°N, 5.61908°E, 31 Oct. 2014, on *Salix*, H. van der Kolk (herb. van der Kolk 272); Boven-Leeuwen, Vogelenzang, 51.88133°N, 5.56269°E, 29 Mar. 2022, on *Fraxinus excelsior*, H. van der Kolk (herb. van der Kolk 2906); Brakel, Waaldijk, 51.82158°N, 5.075°E, 28 Feb. 2022, on *Populus*, C.M. van Herk (herb. van der Kolk 3120); Druten, Heersweg, 51.89151°N, 5.58487°E, 29 Mar. 2022, on *Fraxinus excelsior*, H. van der Kolk (herb. van der Kolk 2908); Eck en Wiel, Rijnstraat, 51.97169°N, 5.44079°E, 11 Mar. 2022, on *Fraxinus*, C.M. van Herk (herb. van der Kolk 3119); Ewijkse Plaat Uiterwaarden, 51.88047°N, 5.75174°E, 7 Sept. 2013, on *Salix*, H. van der Kolk (herb. van der Kolk 115); Groenlo, Ringweg, 52.04744°N, 6.56505°E, 2 May 2022, on *Quercus robur*, H. van der Kolk (herb. van der Kolk 3016); Heerewaarden, De Kop, 51.834°N, 5.3993°E, 22 Feb. 2023, on deciduous tree, H. van der Kolk (herb. van der Kolk 3558); Heerewaarden, De Kop, 51.834°N, 5.3993°E, 22 Feb. 2023, on deciduous tree, H. van der Kolk (herb. van der Kolk 3559); Laren, Holterweg, 52.22303°N, 6.37909°E, 21 Apr. 2022, on *Quercus robur*, H. van der Kolk (herb. van der Kolk 2998); Leuven, Landscheiding, 51.853°N, 5.05707°E, 22 Feb. 2022, on *Populus*, C.M. van Herk (herb. van der Kolk 3118); Lobberdense Waard, 51.88424°N, 6.05422°E, 7 Feb. 2015, on *Salix*, H. van der Kolk (herb. van der Kolk 332); Lochem, 52.13434°N, 6.40821°E, 12 May 2022, on *Quercus robur*, H. van der Kolk (herb. van der Kolk 3037); Millingen, Millingerwaard, 51.87181°N, 6.00392°E, 12 Mar. 2022, on *Salix*, R. van Middelkoop (herb. van der Kolk 2902); Ooijpolder, Groenlanden Zuid, 51.85966°N, 5.90902°E, 5 Mar. 2022, on *Salix*, H. van der Kolk (herb. van der Kolk 2796); Winssen, Haneman, 51.88429°N, 5.69967°E, 8 Apr. 2022, on *Quercus robur*, H. van der Kolk (herb. van der Kolk 2952); Zetten, Onderstalstraat, 51.92238°N, 5.74769°E, 10 Apr. 2022, on *Quercus robur*, H. van der Kolk (herb. van der Kolk 2956). Noord-Brabant, Brabantse Biesbosch, Polder Jantjesplaat, 51.76612°N, 4.75318°E, 1 Oct. 2017, on *Sambucus*, H. van der Kolk (herb. van der Kolk 3054); Dorst, Rijksweg, 51.58792°N, 4.86621°E, 27 Sept. 2023, on *Quercus*, H. van der Kolk (herb. van der Kolk 3808); Lage Zwaluwe, Amerweg, 51.71657°N, 4.70798°E, 12 Aug. 2023, on *Populus*, H. van der Kolk (herb. van der Kolk 3795). Overijssel, Salland, between Wijhe and Heino, 52.41949°N, 6.17447°E, 17 Apr. 2020, on *Quercus*, C.M. van Herk (herb. van der Kolk 3116). Utrecht, Breukelen, De Meent, 52.17404°N, 5.02632°E, 20 Jul. 2018, on *Populus*, C.M. van Herk (herb. van der Kolk 3126); IJsselstein, 52.02559°N, 5.02047°E, 17 Sept. 2018, on *Populus*, C.M. van Herk (herb. van der Kolk 3121); Kockengen, 52.14627°N, 4.92063°E, 22 Mar. 2019, on *Salix*, C.M. van Herk (herb. van der Kolk 3123); Loenen, 52.2019°N, 5.03681°E, 20 Jul. 2018, on *Populus*, C.M. van Herk (herb. van der Kolk 3124); between Harmelen en Kockengen, 52.12591°N, 4.96723°E, 3 Sept. 2018, on *Populus*, C.M. van Herk (herb. van der Kolk 3125); Woudenberg, landgoed De Boom, 52.09624°N, 5.4286°E, 15 Aug. 2018, on *Salix*, C.M. van Herk (herb. van der Kolk 3122). Zeeland, Braakman, 51.32987°N, 3.73031°E, 6 Oct. 2023, on *Acer*, H. van

der Kolk (herb. van der Kolk 3834); Groede, Groese Duintjes, 51.39536°N, 3.48084°E, 8 Oct. 2023, on *Populus*, H. van der Kolk (herb. van der Kolk 3837); Walcheren, Veere, 51.55372°N, 3.64792°E, 4 Jun. 2019, on *Quercus*, C.M. van Herk (herb. van der Kolk 3113); Zeeuws-Vlaanderen, Retranchement, 51.35633°N, 3.38777°E, 24 May 2019, on *Populus*, C.M. van Herk (herb. van der Kolk 3114); Zeeuws-Vlaanderen, Schoondijke, 51.35341°N, 3.53016°E, 21 May 2019, on *Populus*, C.M. van Herk (herb. van der Kolk 3112). Zuid-Holland, Berkheide, 52.17°N, 4.39°E, 1 Apr. 2018, on deciduous tree, T. Naring (herb. van der Kolk 1659); Goedereede, 51.8186°N, 3.97578°E, 15 Jul. 2023, on *Acer*, H. van der Kolk (herb. van der Kolk 3704); Kraansvlak, 52.38769°N, 4.57891°E, 23 Jan. 2023, on *Acer*, H. van der Kolk (herb. van der Kolk 3344); Slikken van Flakkee, 51.76602°N, 4.0372°E, 30 Mar. 2022, on *Salix*, H. van der Kolk (herb. van der Kolk 2920); Slikken van Flakkee, 51.76602°N, 4.0372°E, 30 Mar. 2022, on *Salix*, H. van der Kolk (herb. van der Kolk 2921); Slikken van Flakkee, 51.76602°N, 4.0372°E, 30 Mar. 2022, on *Salix*, H. van der Kolk (herb. van der Kolk 2922); Veermansplaat, 51.75264°N, 3.98229°E, 30 Mar. 2022, on *Salix*, H. van der Kolk (herb. van der Kolk 2917).

Alyxoria varia (Pers.) Ertz & Tehler, Fungal Diversity 49(1): 53. 2011. (Fig. 7)

MycoBank MB 519247

≡ *Opegrapha varia* Pers., Ann. Bot. (Usteri) 7: 30. 1794; *Graphis varia* (Pers.) Wallr., Fl. crypt. Germ. (Norimbergae) 1: 333. 1831.

Type: Europe, C.H. Persoon (L-L0056733 – lectotype!).

= *Opegrapha chlorina* Pers., Ann. Wetter. Gesellsch. Ges. Naturk. 2(1): 15. 1810.

Type: Europe, C.H. Persoon (L-L0056734 – lectotype!).

= *Lichen diaphorus* Ach., Lich. suec. prodr. (Linköping): 20. 1799. ≡ *Opegrapha diaphora* Ach., Methodus, Sectio prior (Stockholmiæ): 19. 1803. ≡ *Alyxoria diaphora* Gray, Nat. Arr. Brit. Pl. (London) 1: 504. 1821.

= *Lichen signatus* Ach., Lich. suec. prodr. (Linköping): 23. 1799. ≡ *Opegrapha signata* (Ach.) Ach., K. Vetensk-Acad. Nya Handl. 30(2): 102. 1809. ≡ *Graphis signata* (Ach.) Wallr., Fl. crypt. Germ. (Norimbergae) 1: 335. 1831.

= *Opegrapha rimalis* Ach., K. Vetensk-Acad. Nya Handl. 30(2): 101. 1809.

= *Opegrapha tridens* Ach., Lich. Univ.: 263. 1810.

Description. Thallus thin, smooth or finely rimose-cracked, white-grey to dark grey, occasionally with a dull brown or light green tinge. Photobiont trentepohlioid. Apothecia always present, scattered or sometimes contiguous, sessile, lirellate, 0.5–1.3(–1.5) × 0.15–0.3 mm, elongate, narrowly ellipsoid or linear, rarely once-branched, exciple margins raised above the disc, slit-like with a narrowly to broadly exposed disc, black, epruinose or rarely with a grey or green pruinose disc. Exciple brown-black in section, K–; hypothecium brown-black, K–; hymenium 60–100 µm, I+ red; epithecium brown, K–. Paraphyses abundant, hyaline, branched. Asci fissitunicate, 45–80 × 12–22 µm, 8-spored. Ascospores 18.1–26.7 × 4.5–6.3 µm, (3–)5–6(–7) septate, narrowly ellipsoidal or somewhat clavate, the middle cell somewhat enlarged, with rounded ends; perispore of ~1 µm, becoming brownish and wrinkled with age. Pycnidia usually present, generally scarce, 70–130 µm, black, epruinose. Conidia hyaline, aseptate, straight, of two types, oblong-bacilliform and 3.7–4.8 × 1.6–2.1 µm, or bacilliform and 3.3–4.5 × 0.9–1.3 µm.

Distribution in Europe. Widespread in Europe, known from many countries including Norway, Sweden, Germany, the Netherlands, Belgium, Great Britain, Ireland, France, Spain, Portugal, Italy and Greece.

Ecology and habitat. Usually on dry bark of deciduous trees in woodlands, sometimes also in parks or on roadside trees, usually on *Carpinus*, *Fagus*, *Fraxinus* and *Quercus*.

Notes. Typical specimens have a grey-white, thin thallus, little pycnidia and abundant, relatively large, elongated apothecia (Fig. 7C, D). Sometimes pycnidia are abundant (Fig. 7E, F). In some specimens the apothecia are relatively short (Fig. 7G, H), and those morphs resemble *Alyxoria lichenoides*. We always recommend microscopic examination of the conidia and ascospores to confirm the identification of *Alyxoria varia*, since besides *Alyxoria lichenoides* it can also be confused with other *Alyxoria* species. Typical forms of *Alyxoria varia* are macroscopically very similar to *Alyxoria culmigena* and *Alyxoria ochrocheila*, but differ in that the latter two species have 3-septate ascospores. *Alyxoria culmigena* usually has no pycnidia. *Alyxoria ochrocheila* has a more distinct thallus under similar conditions, and slightly smaller lirellae.

Many records of *Alyxoria varia* belong to *A. lichenoides* (see notes under *A. lichenoides*). Many names have been described in the past that are now considered synonyms of *Alyxoria varia*. For example, *Opegrapha diaphora* and *Opegrapha rimalis* were separated based on the dimensions of the conidia, *Opegrapha diaphora* being the name for the broad type of conidia and *Opegrapha rimalis* for the narrow type of conidia of *Alyxoria varia* (Erichsen 1957). *Opegrapha chlorina* should also be considered a synonym of *Alyxoria varia*.

Specimens examined. AUSTRIA. Steiermark, Graz, Raabklamm, 47.236°N, 15.5542°E, 1 Jul. 2022, on *Acer pseudoplatanus*, H. van der Kolk (herb. van der Kolk 3108); Graz, Raabklamm, 47.2354°N, 15.5564°E, 1 Jul. 2022, on *Corylus*, H. van der Kolk (herb. van der Kolk 3109). FRANCE. Jura, villa palladienne à Syam, 25 Aug. 2016, on *Tilia*, C. Van Haluwyn (herb. Van Haluwyn 335). Nord, Liessies, l'Abbaye de Liessies, 14 May 2022, on *Malus*, G. Polesel 8i; Wallers-en-Fagne, Monts de Baives, 20 Aug. 2020, on *Tilia cordata*, Benoît Toussaint; Le Cateau Cambrésis, jardin public Fénelon, 19 Aug. 2020, on *Tilia*, C. Van Haluwyn (herb. Van Haluwyn 1028). Pas-de-Calais, Forêt d'Hesdin, 26 Aug. 2022, on *Fagus*, G. Polesel 26C. NETHERLANDS. Gelderland, Dreumel, uiterwaarden, 51.86733°N, 5.43731°E, 3 Mar. 2022, on *Populus*, C.M. van Herk (herb. van der Kolk 3117); Landgoed Staverden, 52.28469°N, 5.73695°E, 14 Dec. 2022, on *Magnolia*, H. van der Kolk (herb. van der Kolk 3286); Paleispark het Loo, 52.23472°N, 5.94182°E, 17 Apr. 2023, on *Fagus*, H. van der Kolk (herb. van der Kolk 3488); Putten, Speulderbos, 52.2561°N, 5.66478°E, 29 Jul. 2023, on *Fagus*, H. van der Kolk (herb. van der Kolk 3732); Putten, Speulderbos, 52.25822°N, 5.66408°E, 29 Jul. 2023, on *Fagus*, H. van der Kolk (herb. van der Kolk 3733); Vierhouten, Vierhouterbos, 52.31714°N, 5.871°E, 18 Feb. 2025, on *Fagus*, H. van der Kolk (herb. van der Kolk 4539). Utrecht, Amerongen, kasteeltuin, 51.9965°N, 5.45746°E, 21 Jan. 2023, on *Carpinus*, H. van der Kolk (herb. van der Kolk 3324); Amersfoort, Nimmerdor,

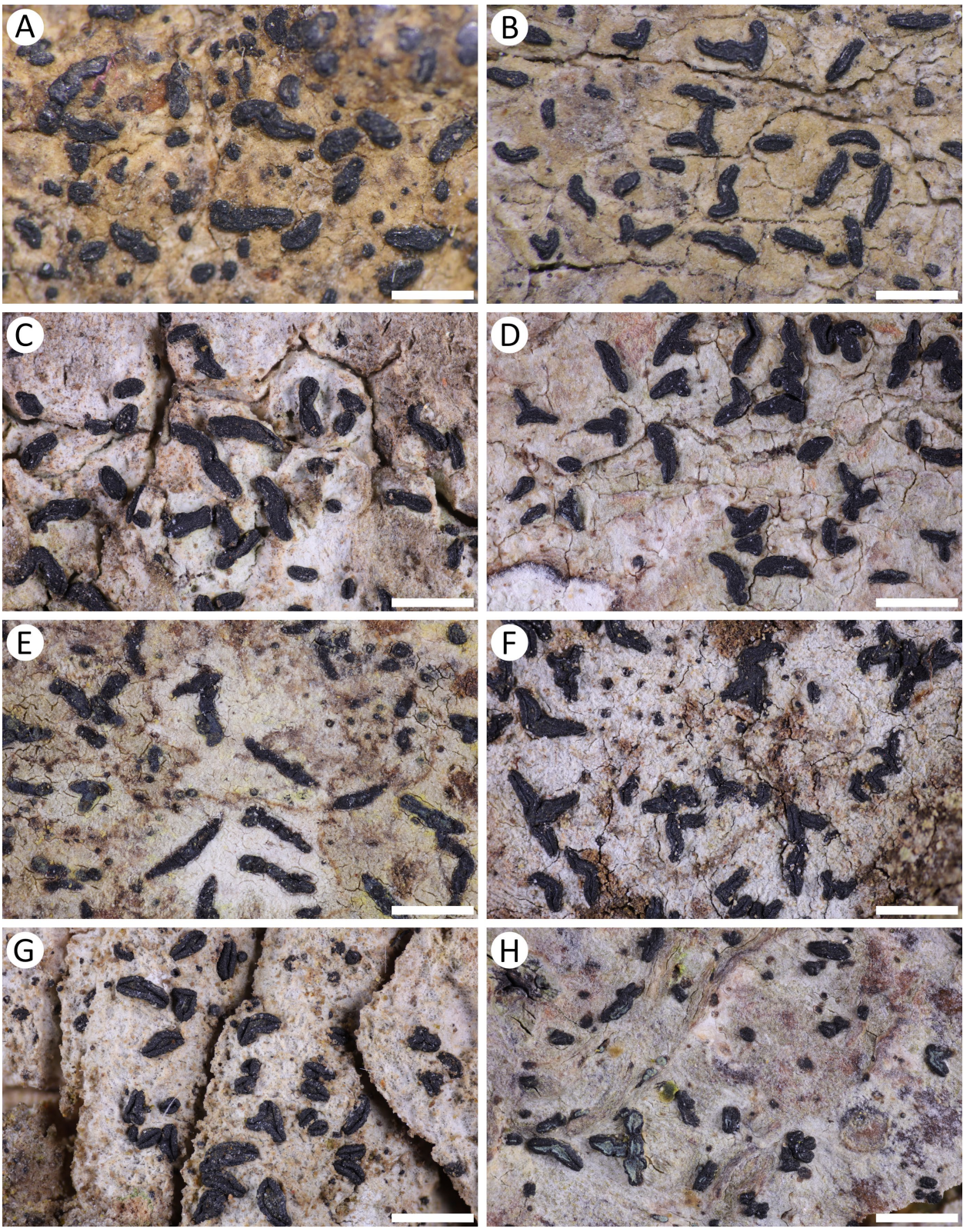

Figure 7. *Alyxoria varia*. A – lectotype of *Alyxoria varia* (L0056733); B – lectotype of *Opegrapha chlorina* (L0056734); C – van der Kolk 4697; D – van der Kolk 3108; E – van der Kolk 481; F – van der Kolk 3527; G – van der Kolk 3117; H – van der Kolk 3733. Scales: A–H = 1 mm.

52.13438°N, 5.38371°E, 12 Apr. 2021, on *Fagus*, N. Buddingh (herb. Verboom 461); Baarn, Paleis Soestdijk, 52.19513°N, 5.27728°E, 29 May 2023, on *Liriodendron*, H. van der Kolk (herb. van der Kolk 3527); Doorn, huis Doorn, 52.03°N, 5.24°E, 29 Jan. 2021, on *Quercus*, L. Verboom (herb. Verboom 206); Leersum Broekhuizen, 52.008°N, 5.402°E, 5 Mar. 2016, on *Fagus*, H. van der Kolk (herb. van der Kolk 481). PORTUGAL. Alentejo, Odemira, Pego das Pias, 37.6335°N, 8.6243°W, 25 Dec. 2024, on *Fraxinus*, H. van der Kolk (herb. van der Kolk 4696); Sao Luis, 37.7188°N, 8.6767°W, 28 Dec. 2024, on *Quercus suber*, H. van der Kolk (herb. van der Kolk 4697).

Alyxoria viridipruinosa (Coppins & Yahr) Ertz, Bull. Soc. Nat. luxemb. 113: 105. 2012. (Fig. 8)

MycoBank MB 801452

≡ *Opegrapha viridipruinosa* Coppins & Yahr, Phytotaxa 18: 90. 2011.

Type: England, East Suffolk, Needham Market, 52°9′N, 1°4′E, on *Sambucus* bark in sheltered, disused chalk pit, June 2004, Earland-Bennett & Hitch s.n. (E – holotype).

Description. Thallus thin, smooth or sometimes slightly cracked, white-grey to light brown, often covered with yellow-green pruina (K+ yellow in section). Photobiont trentepohlioid. Apothecia frequently present, scattered or sometimes contiguous, sessile, lirellate, 0.20–0.55 × 0.08–0.23 mm, narrowly ellipsoid, elongate or stellate,

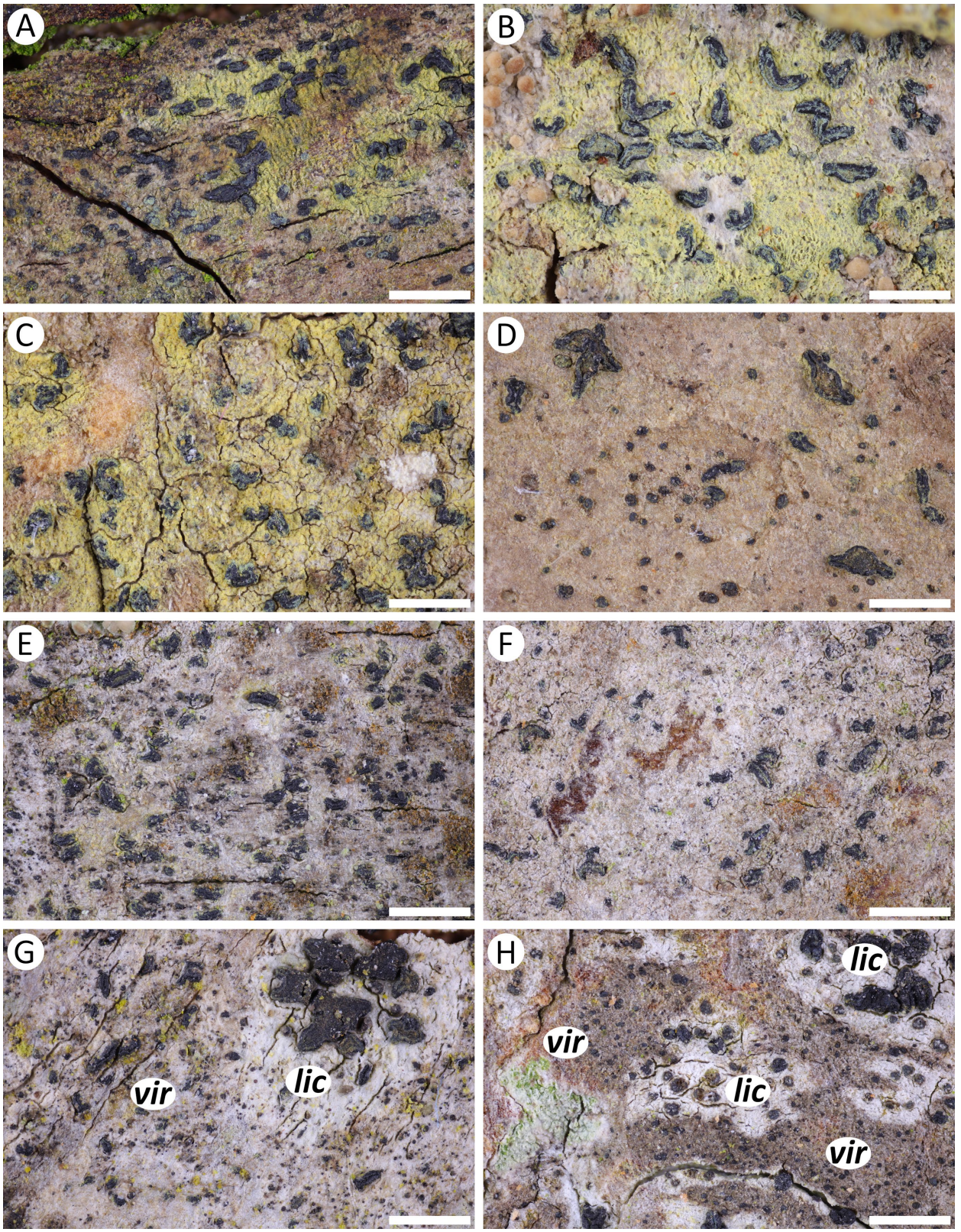

Figure 8. *Alyxoria viridipruinosa*. A – Verboom 3402; B – van der Kolk 3053; C – van der Kolk 1068; D – van der Kolk 3115; E – Verboom 2824; F – Verboom 3119; G – *Alyxoria lichenoides* (lic) and *A. viridipruinosa* (vir), van der Kolk 4719; H – *Alyxoria lichenoides* (lic) and *A. viridipruinosa* (vir), Verboom 2872. Scales: A–H = 1 mm.

unbranched or once-branched, exciple margins raised above the disc, slit-like without or with narrowly (rarely broadly) exposed disc, black, epruinose or yellow-green pruinose. Exciple brown-black in section, K–; hypothecium brown-black, K–; hymenium 40–70 µm, I+ red; epithecium brown, K– (but green-yellow pruina, when present, faintly K+ yellow). Paraphyses abundant, hyaline, branched. Asci fissitunicate, 30–60 × 11–16 µm, 8-spored. Ascospores 13.7–20.6 × 3.5–5.4 µm, (2–)3–4(–6) septate, narrowly ellipsoidal, with rounded ends; perispore of ~1 µm, becoming brownish and wrinkled with age. Pycnidia always present, scarce to numerous, (20–)40–110(–160) µm, black, epruinose or sometimes green-pruinose. Conidia bacilliform to narrowly ellipsoid, hyaline, aseptate, straight or slightly curved, 3.0–3.7 × 1.0–1.4(–1.5) µm.

Distribution in Europe. Currently known from Great Britain (Lumbsch et al 2011), the Netherlands, and France (Roux et al., 2025). Records from Germany (Schiefelbein et al. 2014) need confirmation.

Ecology and habitat. On the trunks of trees in sheltered situations, as well as on the north side of roadside or woodland trees. Most common on *Acer campestre*, *Populus*, *Quercus*, *Sambucus* and *Tilia*. In the Netherlands mostly restricted to coastal areas.

Notes. *Alyxoria viridipruinosa* is the smallest of the discussed species, and many morphs are easily overlooked due to their inconspicuous thallus, small pycnidia and small apothecia. It is an extremely variable species with respect to thallus color and the exposure of the discs of the apothecia. The presence of yellow-green pruina is not a useful characteristic to separate this species from *Alyxoria lichenoides*. According to our observations, yellow-green morphs (Fig. 8A–C) are more common in moist woodland areas, whereas morphs with whitish or brownish thallus (Fig. 8D–F) occur on roadside trees in drier conditions.

Alyxoria viridipruinosa often grows together with *Alyxoria lichenoides* (Fig. 8G, H), and can then be recognized by its thinner thallus, smaller pycnidia and smaller, thinner lirellae. On wayside trees it seems to be less tolerant of exposure to wind and direct sunlight than *A. lichenoides*, and it is usually found on the northeastern facing base of the tree trunk side.

Our measurements show that the conidia are slightly larger than the dimensions reported in the original description (2.5–3 × 1–1.3 µm; Lumbsch et al. 2011), but we have no doubt that our specimens represent the same species. The measured dimensions of the apothecia of *Alyxoria viridipruinosa* match well with the dimensions reported in the original description (0.3–0.6 × 0.1–0.3; Lumbsch et al. 2011).

Specimens examined. NETHERLANDS. Friesland, Westergeest, 53.29031°N, 6.08533°E, 1 Nov. 2025, on *Tilia*, L. Verboom (herb. Verboom 3119). Gelderland, Beesd, Tiendweg, 51.89776°N, 5.14525°E, 7 Aug. 2024, on *Populus*, H. van der Kolk (herb. van der Kolk 4719); Spijk, 51.85722°N, 5.00827°E, 28 Dec. 2017, on *Fraxinus*, H. van der Kolk (herb. van der Kolk 1068). Noord-Brabant, Brabantse Biesbosch, Polder Jantjesplaat, 51.76612°N, 4.75318°E, 1 Oct. 2017, on *Sambucus*, H. van der Kolk (herb. van der Kolk 3053). Noord-Holland, Amsterdam, Oeverlanden Noord, 52.33522°N, 4.82705°E, 1 Feb. 2026, on *Salix*, L. Verboom (herb. Verboom 3402); Zaandam, 52.4273°N, 4.84583°E, 5 Dec. 2019, on *Acer*, H. van der Kolk (herb. van der Kolk 1709). Zeeland, Hoek, Lovenweg, 51.32912°N, 3.7891°E, 7 Oct. 2025, on *Populus*, H. van der Kolk (herb. van der Kolk 4707); ‘s-Gravenpolder, Slabbekoornsedijk, 51.44456°N, 3.91909°E, 09 oktober 2025, on *Populus*, L. Verboom (herb. Verboom 2872); Vrouwenpolder, Rijkebuurtweg, 51.56608°N, 3.62043°E, 25 Sept. 2025, on *Populus*, L. Verboom (herb. Verboom 2897); Walcheren, Vrouwenpolder, Oranjezon, 51.59012°N, 3.57879°E, 28 Jun. 2019, on *Quercus*, C.M. van Herk (herb. van der Kolk 3115); Westkapelle, Pauluswegeling, 51.52738°N, 3.45366°E, 26 Sept. 2025, on *Populus*, L. Verboom (herb. Verboom 2824); Zeeland, Zaamslagveer, Catharinapolder, 51.29158°N, 3.97945°E, 8 Oct. 2025, on *Populus*, H. van der Kolk (herb. van der Kolk 4706); Zuid-Beveland, Rilland, 51.40879°N, 4.24854°E, 15 Apr. 2019, on *Populus*, C.M. van Herk (herb. van der Kolk 3111). Zuid-Holland, Alphen aan den Rijn, 52.15462°N, 4.64591°E, 21 Aug. 2025, on *Quercus robur*, L. Verboom (herb. Verboom 2718).

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Data availability

All individual measurements are released in a dataset on Zenodo accessible via https://doi.org/10.5281/zenodo.20314363.

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