

Downy Mildews (Peronosporaceae) and White Blister-rusts (Albuginaceae) of Wales

Llwydni Gwlannog (Peronosporaceae)

a Rhydau-Pothelli

Gwynion (Albuginaceae) Cymru

Arthur O. Chater, Ray G. Woods, R. Nigel Stringer, Debbie A. Evans & Paul A. Smith

Summary

The downy mildews and white blister-rusts are specialist plant pathogens, which, although they are fungus-like, are no longer considered to be related to fungi. They are now placed in the Kingdom Chromista. In Wales 133 different taxa have been recorded in 268 combinations with hosts. Whilst most plants appear to survive alongside these fungus-like organisms, some downy mildews can cause economic loss in crop plants whilst others may help shape ecosystems.

This publication seeks to stimulate an interest in them, facilitate their identification and review our current knowledge of their abundance and distribution in Wales.

Crynodeb

Mae y llwydni gwlannog a rhydau-pothelli gwynion yn bathogennau arbennigol ar blanhigion, ac er eu bod yn debyg i ffwng nid ydynt yn cael eu ystyried yn perthyn i'r ffwng bellach. Maent yn awr yn cael eu gosod yn y Deyrnas Chromista. Cofnodwyd 133 tacsa o wahanol fath yng Nghymru mewn 268 o gyfuniadau gyda planhigion lletuol. Tra bod y rhan fwyaf o blanhigion yn ymddangos i oroesi ynghyd a'r organebau fel-ffwng yma, gall rhai llwydni gwlannog achosi colledion economaidd mewn cropiau tra gall eraill roi cymorth i roi strwythyr i ecosystemau.

Mae'r cyhoeddiad yma yn anelu i ysgogi diddordeb ynddynt, rhoi cymorth i'w adnabod ac adolygu ein gwybodaeth gyfoes am eu niferoedd a'u dosbarthiad yng Nghymru.

Cover Stories

The front cover displays images of (top left) *Trifolium medium* Zig-Zag Clover with yellow streaked foliage caused by *Peronospora trifoliorum*. Top right are the sporangiophores of *Peronospora viciae* on a leaf of *Vicia orobus* Wood Bitter-vetch in an Elan Valley hay meadow in Radnorshire. Bottom left is a leaf of *Sisymbrium officinale* Hedge Mustard with the white pustular sporangiophores of the blister-rust *Albugo candida* s.l., whilst bottom right is a sporangiophore and sporangia of *Hyaloperonospora sisymbrium-loeselii*.

The rear cover displays images of *Succisa pratensis* Devil's-bit Scabious on which diligent searching revealed the presence of *Peronospora violacea* in a number of sites in Mid and West Wales. It turns the infloresceses prematurely brown (centre image). The sporangiophores (lower left) can erupt from any part of the flowers whilst the overwintering oospores (upper right) fill the cells of the corolla.

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"This fading part [of Garden Pea with downy mildew] is caused by the Peronospora, which is luxuriating in the lower part, and is drawing away the vitals of its host. Get a pin or a sharply-pointed knife and put an atom in a drop of water on a glass for examination under the microscope, and if you see no beautiful plants there, as well-developed as an oak tree, and as perfect in structure as the oak, bless your stupidity. You have been born in vain."

(Vize 1894)



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Preface

This is a Census Catalogue and guide to the downy mildews and white blister-rusts of Wales. For the principality it updates and expands on Tom Preece's "A Checklist of the Downy Mildews (Peronosporaceae) of the British Isles", published in 2002. Since this checklist was published, modern DNA analysis has greatly narrowed species concepts and revolutionized our understanding of the evolutionary relationship of the group to the rest of the living world. They were considered to be fungi, but detailed genetical studies have established their origins not with the fungi but closer to such unlikely relatives as the brown seaweeds. They are currently placed in the Kingdom Chromista. Relatives also include the rest of the water moulds and most significantly the *Phytophthoras*, groups we have not covered here. Many can be serious pathogenic organisms, the drivers of evolution of their hosts and some of them cause diseases of agricultural and horticultural significance. We ignore them at our peril.

Acknowledgements

We are grateful to Tom Preece for guidance and literature in the early stages of the preparation of this book, and Marco Thines for recent updates and advice. Chris Preston has helped us in the field and has made valuable comments on the text; Brian Spooner has helped with useful information. Alan Orange has abstracted information from the collections in the National Museum of Wales. Various people have collected material for us in the field, including Julian Woodman, Theresa Greenaway, Andy Jones, David Mitchel, Joe Weightman and Matt Sutton. We also thank the Royal Horticultural Society for permission to reproduce some of their images and Eilir Evans for providing the Welsh translations.



Left: Sporangiophore and oospores of *Peronospora violacea* from an inflorescence of *Succisa pratensis* Devil's Bit.

Centre: White blisters of Albugo candida s.l. on Brassica oleracea var. viridis Kale.

Right: Sporangiophore of Peronospora alsinearum.

Introduction

The downy mildews (**Peronosporaceae**) and white blister-rusts (**Albuginaceae**) belong to the class **Oomycota** (sometimes now referred to the Oophyceae) in the kingdom **Chromista**. Their relationship to one another is still the subject of debate, and some authors place them together within the Order **Peronosporales**. Among other differences from fungi, their cell walls are of cellulose and glycan rather than of chitin. All are obligate parasites of angiosperms and many cause diseases of commercial significance.

Infected crop plants range from Lettuce, Cabbage, Beet and Onions to Hops and Grape-vines. A chance observation by Millardet in France in 1882 led to the discovery of Bordeaux mixture as a means of controlling an outbreak of downy mildews on vines that threatened the French wine industry. Rows of grapes next to a public footpath had been sprayed with copper acetate (verdigris), making the grapes bitter to deter pilfering. These grapes resisted infection by downy mildew (Large 1940, Ingram & Robertson 1999), and Bordeaux mixture as a fungicide was used thereafter for many decades. Quite how significant downy mildews were to Welsh agriculture in the past we may never know since all the records for Wales, carefully collated by the Ministry of Agriculture, Fisheries and Food over many years have apparently been destroyed (Preece 2002).

Nomenclature and taxonomy of these mildews are currently in a state of flux; this account largely follows Klenke & Scholler (2015), where many more species are recognized than in the Fungus Records Database of Britian and Ireland (FRDBI). The former is currently the essential and indeed only manual for identification. Surprisingly there is no modern monograph, but recently many new species have been described, indicating considerable host specificity allied with molecular features (Göker et al. 2009). As a result of DNA technology, genera such as *Bremia*, *Albugo* and *Pustula* in particular are likely to be further split up in the future.

Nomenclature, including English names, and taxonomy of the hosts in this account mostly follow Stace ed. 4 (2019), although extra infraspecific taxa are sometimes indicated. Older records of species that have now been split up have had their identities updated for this account, in so far as this has been possible from a knowledge of the host plant. We have of necessity assumed that the downy mildew genus, and indeed the host plant, were correctly identified in the first place. Selected synonyms are given in the text where this is helpful. Much of interest about the downy mildews can be found in published works such as those of Moore (1959), Spencer (1981), Dick (1981), Ingram & Robertson (1999) and Lebeda *et al.* (2008). Several websites, including Plant Parasites of Europe https://bladmineerders.nl/, include photographs and descriptions (in English) of a number of species found in Wales, and there are many good illustrations in Kruse (2019). Many species are considered to be gall-causers, and information on them from this perspective can be found in Redfern *et al.* (2011), Spooner (2017) and Roskam (2019). Preece (1996) provides a useful guide to downy mildews, powdery mildews, smuts and rusts for anyone commencing a study of plant parasites.

The terminology for the anatomy of downy mildews and white blister-rusts originates in their earlier treatment as fungi, though the various organs are not homologous.

The annotations in the species accounts below, in so far as they are descriptive, are based chiefly on observations made in Wales. Distributional information is summarized by reference to the Watsonian vice-counties (Watson 1883). The most detailed studies have been carried out in Radnorshire VC43, Carmarthenshire VC44, Cardiganshire VC46, Caernarvonshire VC49 and Anglesey VC52 but the observations can probably be considered to have wider application.

Identification

Although many identifications can be made with a fair degree of certainty using the present account, we strongly recommend that Klenke & Scholler (2015) (in German) is used as the currently best available guide. Ellis & Ellis (1997) is very incomplete and now out of date. A good identification guide to the host species is essential (we have used the taxonomy of Stace (2019) here) and Poland & Clement (2020) is helpful, especially where the infection has inhibited flowering.

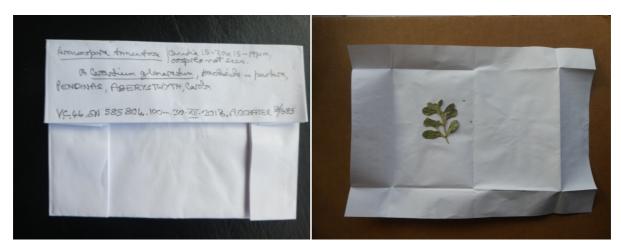
Identification for the ordinary recorder not using molecular techniques requires only very straightforward microscope work. Fresh material is better to work on, but properly preserved specimens (see below for details) are usually adequate. Sporangiophores and sporangia can easily be moved onto a slide with a needle, or transferred on transparent sticky tape such as Scotch Tape or Sellotape: a small piece of tape is pressed onto the leaf, peeled off, and wetted in a drop of water on a slide; it is then turned over so that the sticky side with the mildew is uppermost, replaced submerged in the drop and a coverslip added. Should the tape curl up on being wetted we recommend you change to a different brand. Slight variations in method are described in Evans (2013) and Leech (2017). Oospores can be searched for with a needle and forceps to mash up fragments of tissue from beneath areas of sporangiophores or from other discoloured parts of the host, or sometimes from other apparently unaltered parts of the host; care should be taken that only mature oospores are measured. Haustoria can be searched for in the same way, but are usually elusive.

The identification of the *Peronospora* species on *Trifolium* Clovers is particularly confusing, and Klenke & Scholler (2015), for reasons unstated, do not accept the taxonomy of Garcíá-Blazquez *et al.* (2008) which is based on molecular evidence; such discrepancies are noted in the species accounts below.

Collection and Preservation

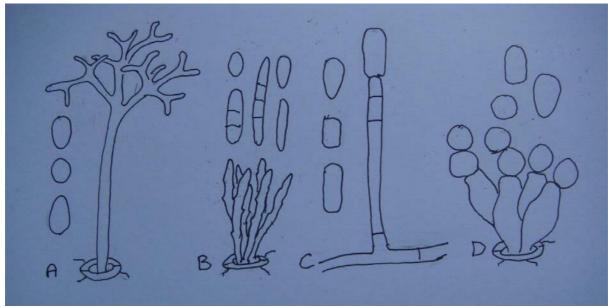
Maintaining a collection of material is essential: it enables revision of one's determinations, especially if the taxonomy is changed, it enables comparisons to be made and it can be a valuable source of material for DNA studies. A characteristic sample of the infected part of the host, such as a whole leaf or leaves, should be packeted and dried in a press as one does with plants in general, either changing the drying paper or using gentle heat. It is helpful not to preserve too much material in a sample so as to discourage grazing invertebrates and growth of other moulds. Packets should be of a standard size for ease of filing, and labelled with name of mildew, name of host, habitat, location, grid reference, altitude, date and collector. Any observations on abundance, measurements, other details observed under the microscope and anything else of interest should be added. Pencil is

more permanent than most inks, many of which fade even in the dark. A6 is a convenient size for the packets, and they can be folded from an A4 sheet so as to enclose the specimen safely protected from spillage or the attentions of mites or other pests (see illustrations below). Ideally archive quality paper should be used.



Packets should be stored in dry conditions, checked regularly to ensure no invertebrates have gained access or saprotrophic fungi have started to grow on the specimens. Both can be controlled by placing the packets in sealed containers in a deep freeze for two weeks.

Having successfully collected, preserved and packeted your specimen a small sample can then be mounted under the microscope. Assuming your collection was of a grey, white or purplish mould from living or chiefly living plant material (there are lots of different fungi that live on dead and decaying plant material, which are not considered here) you may have collected material that matches one of the drawings below. Branched sporangiophores with single celled oval or globose sporangia (see A below) and a non septate mycelium are of a member of the downy mildews Peronosporaceae. Fungi in the genus *Ramularia* may look similar in the field but under the microscope their clustered, mostly unbranched conidiopores (see B below) cannot be mistaken for the tree-like sporangiophores of downy mildews and their conidia are often septate. Powdery mildews (in the Erysiphales) almost always display

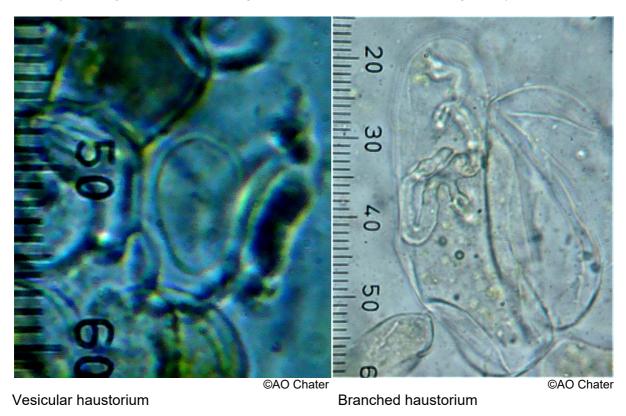


© AO Chater

an extensive superficial mycelium on the leaf surface never present in downy mildews and their conidiophores are unbranched and septate (see C above). In the white blister-rusts Albuginaceae sporangiophores are very short, clavate and entire, budding off the sporangia at the apex (see D above).

The Downy Mildews - Peronosporaceae

Out of 152 species in the Peronosporaceae recorded from Britain, we have traced records of 123 species from Wales, in eight genera – *Bremia, Hyaloperonospora, Paraperonospora, Perofascia, Peronospora, Plasmopara, Plasmoverna* and *Pseudoperonospora*. The mycelium is within the plant tissue and the hyphae are aseptate. Haustoria, produced within the host cells and absorbing nutrients from the host, are hypha-like in some genera (see image below right of host cell with a branched hypha-like haustorium inside) and vesicular in others (see image below left of a large vesicular haustorium part filling a cell).



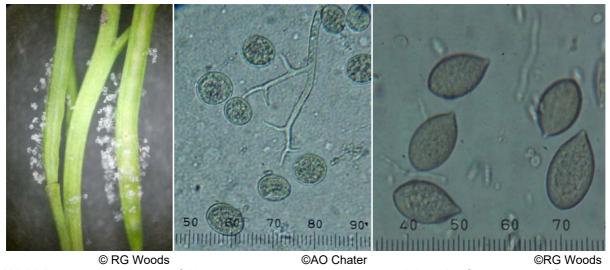
Sporangiophores bearing the sporangia emerge mostly through the stomata and are repeatedly branched dichotomously or irregularly branched in the upper part (see image opposite). These pale-coloured, tree-like structures distinguish the downy mildews from other plant parasites. The sporangia of downy mildews produce germ tubes in some genera and zoospores in others. They are usually confined to the lower surface of the leaves, but sometimes also develop on bracts, calyces, corollas and stems, and their growths are referred to as "colonies".



Sporangiophore of *Peronospora viciae* with sporangia above left. Sporangiophores on both upper and lower surfaces of leaf of *Vicia orobus* above right.

The only host plants in Wales with stomata confined to the upper surface of the leaves (see Poland & Clement 2020) are *Vicia orobus* Wood Bitter-vetch, on which *Peronospora viciae* s.l. occurs, and *Euphorbia paralias* Sea Spurge, on which *P. euphorbiae* occurs elsewhere in Britain. In *Vicia orobus* sporangiophores are as expected abundant on the upper surface, but also emerge less abundantly on the lower surface, breaking through the epidermis perhaps where it is weakened by the infection; it is not recorded how and where the sporangiophores emerge in *Euphorbia paralias*.

The sporangia provide most of the colouring to the colonies, which is best seen in reflected light by means of a hand lens or a stereo microscope, and does not show well in transmitted light under a compound microscope. Almost always there is corresponding discoloration visible on the upper leaf surface, and often deformation, making infected plants fairly easily



Whitish sporangiophores of *Hyaloperonospora nasturtii-aquatici* on the flower stem of *Cardamine hirsuta* above left. Above centre and right are downy mildew sporangia. *Peronospora obovata* centre and *Hyaloperonospora sisymbrii-loeselii* right.

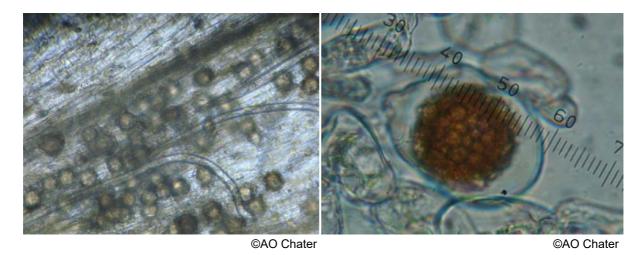
noticeable. Usually this starts pale or yellowish, then darkens and becomes brownish as necrosis sets in. It should be noted though that host discolouration is more related to physiological condition of the host and may often not be due to the mildew; damage to the tissue of any particular host by downy mildews, fungi, invertebrates or physical accidents usually results in the affected parts of the leaf colouring up in the same way. Leaves and shoots of many species suffer similar discolouration and deformation of the plant following aphid attack and must always be carefully examined to establish the presence of the mildew.

In the Peronosporaceae, the asexually produced sporangia are normally dispersed in the air. They can vary in shape from globose to lemon-shaped (see images centre and right above). When they land on a suitable leaf surface they either produce germ tubes that enter the leaf via the stomata or by breaking through the cuticle, as is the case in *Bremia*, *Hyaloperonospora*, *Paraperonospora* and *Peronospora*; or they produce motile zoospores that encyst after dispersing and then produce a germ tube that gains entry in the same way, as is the case in all the other genera. Asexual spores producing germ tubes are technically known as conidia, but in the downy mildews, as many genera have true sporangia that produce zoospores rather than germtubes, these asexual spores are all called sporangia for convenience.



©AO Chater ©AO Chater Image above left is of a sporangium with a germ tube, whilst to the right a sporangium germinates to produce zoospores.

Sporangia and zoospores are short-lived, but within the host tissue many species can develop antheridia and oogonia on the hyphae from which thick-walled resting oospores are produced by sexual reproduction (see images opposite of oospores of *Peronospora conferta* to the right and *P. violacea* to the left). These can be found in the plant tissue, although they

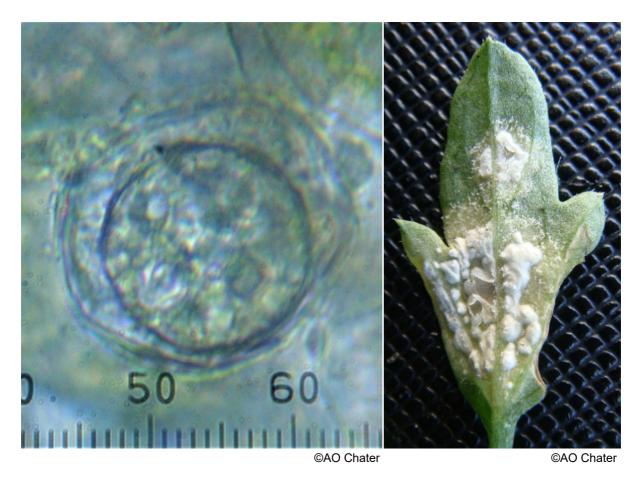


are often not produced and are not always in the same parts of the host as the sporangiophores develop from. They are dispersed when the tissue decays.

The White Blister-Rusts – Albuginaceae

Two genera, *Albugo* and *Pustula*, and ten taxa of Albuginaceae have been reported from Britain. All occur in Wales. They differ chiefly from the Peronosporaceae in that the sporangiophores are very short, clavate and entire, budding off the sporangia at the apex (see image below right) and form a dense powdery mass in distinct sori under the cuticle of the host leaf so that the colonies have a shiny white or yellowish crust (see image below left of blisters of *Albugo candida* s.s. on an *Erophila* sp. Whitlowgrass leaf). The haustoria are globose and small.





The sporangia produce motile zoospores and not germ tubes and resting oospores are also usually produced within the tissue of the host (see image above left).

Sansome & Sansome (1974) found that sexual reproduction leading to the production of oospores was rare in *Albugo* on *Capsella* Shepherd's-purse, but when it was present it occurred all over the infected parts of a plant, suggesting that *Albugo candida* is heterothallic, with complementary mating types. It was also more frequent when there was a concomitant infection of the downy mildew *Peronospora parasitica* (i.e. *Hyaloperonospora parasitica*), suggesting that sexual reproduction may also be stimulated by the presence of the complementary mating type of another genus. Ingram & Robertson (1999) describe this coexistence as often occurring. In Wales, colonies of *Albugo* and *Hyaloperonospora* have occasionally been recorded as adjacent or mixed together, for example *A. candida* s.l. and *H. nasturtii-aquatici* colonies abutting on each other on leaves of *Cardamine flexuosa* Wavy Bitter-cress at Llanelli, Carms (see image above right).

Epidemiology

Many or most species tend to occur early in the year, and abundance varies enormously from year to year, presumably in relation to weather, damp or wet and mild conditions being favourable. Most species require high humidities for spore germination. In 2017 and 2018 few downy mildews were seen, and some of the normally commonest species were seen only a handful of times or not at all, whereas in 2019 they were strikingly common in some areas. At the end of each species account below, the range of months simply indicates when

there have been records in Wales, and the species doubtless often occur outside these ranges.

The dispersal and epidemiology of downy mildews is in most cases not properly understood, but in general, long distance spore dispersal is by air, although localised dispersal can be by 'splash dispersal' by rain droplets. More is known though about many of the agriculturally significant species. An example of this is *Pseudoperonospora humuli*, attacking Hops, whose history is summarized by D. J. Royle & H. T. Kremheller in Spencer (1981). The disease was first reported in Japan in 1905 on both wild and cultivated Hops, and then appeared on wild Hops in the USA in 1909. After an eleven-year apparent disappearance it was reported from Devon in England on wild Hops, and appeared on both wild and cultivated Hops in many European countries through the 1920s, causing immense damage. It started attacking cultivated crops in the USA in 1928, causing over 30% of crop losses. Widespread research recommended changes in cultivation methods, the use of sprays, and the breeding of resistant cultivars, and the mildew, though still prevalent and economically significant, is now more controllable. Study of airborne spore concentrations and weather conditions can enable forecasting of infections so that control methods, notably sprays, can forestall them.

Finding Downy Mildews and White Blister-Rusts

As well as discolouration and distortion of leaves and stems, another useful sign of infection is that leaves, especially of rosettes, are often held unusually erect and sometimes on elongated petioles. This clearly facilitates the spread of sporangia. It can also be useful to dissect necrotic tissue of likely hosts as this may contain evidence of a mildew.

M.C. Cooke in his excellent guide to microscopic fungi of 1898 provides the following sage advice equally applicable today to anyone intent on finding mildews. "Those who attempt it must be prepared to sacrifice their kid gloves and patent leather boots, to put on waterproofs and perseverance and come home sometimes disappointed. The requisites for good work are but few and easily supplied. A strong knife, a pocket lens, and a box or leather bag will be all that is really essential. But where shall we go----and when? Hedge-banks, the sides of ditches, borders of woods, anywhere, if the plants are to be found on which the fungi [sic] are parasitic. We flatter ourselves on being rather successful in collecting and our favourite localities have always been the dampest places in woods, railway banks and waste places. It is a great mistake to endeavor to go over a large tract of ground. We have spent a whole day in a little chalkpit. Fifty yards into a wood is as much as we attempt and a spot six yards square has afforded us occupation for hours. It is better to examine a small space thoroughly than to scamper on, mile after mile and find nothing.

When?...So long as the ground is not covered with snow there will always be something to find".

To his advice we might add that a good identification guide to the host species is essential. Should there be uncertainty about the host, adequate material should be collected to permit later identification. In searching for these organisms, it is worth bearing in mind that, of the host species and hybrids that support downy mildews and white blister-rusts in Wales, 101 (55%) are perennials (7 of these being woody), 18 (10%) are biennials and 64 (35%) are annuals. The corresponding numbers for powdery mildews are 285 (76%) perennials (97

woody), 26 (7%) biennials and 65 (17%) annuals and the distribution of the types of mildews over life forms is statistically different (p < 0.0001). The preponderance of annual hosts of downy mildews is notable. This is perhaps connected with discoveries reviewed by Ingram & Robertson (1999) that cotyledons are often the most susceptible parts of a plant to infection by white blister-rusts and downy mildews. Annuals (and ephemerals) with their short life cycles produce cotyledons more frequently and over time in greater numbers, which can profitably be searched; brown field sites, waste ground and weedy arable fields are especially productive. *Buddleja davidii* Butterfly Bush, *Prunus laurocerasus* Cherry Laurel, *Rosa* spp. Roses, *Rubus* spp. Brambles, *Veronica* subgenus *Pseudoveronica* Hebes and *Vitis vinifera* Grape-vine, are the only woody hosts recorded in Wales. No species occur on Poaceae Grasses in Britain (in stark contrast to the diversity of rusts and smuts on these hosts (Woods *et al.* 2015, 2018)), although the downy mildew *Sclerophthora macrospora* occurs on *Lolium* Rye-grasses, *Phleum* Cat's-tails, *Triticum* Wheats, and a few other grasses in Central Europe and on other species in further parts of the world. No species occur on pteridophytes or conifers anywhere.



The illustrations above typify two habitats rich in downy mildews in Wales. Above left illustrates the wide fallow margins with arable weeds around a mixed cereal crop grown specifically to feed wild birds as an option in an agri-environment scheme near Clyro, Radnorshire. Over a dozen downy mildews were recorded in this field. Above right are the dunes at Ynyslas, Cardiganshire, where a similar number of species have been recorded.

History of Recording and Development of a Welsh Census Catalogue



There have been very few historic studies of this group of organisms in Wales, but an outstanding early contributor was the **Rev. John Edward Vize** (left). Previously an accomplished conchologist, he became interested in fungi and downy mildews when he began a curacy at Forden, between Montgomery and Welshpool, in 1867. He was appointed vicar there in 1873, and lived at Forden for the rest of his life. His career is covered in several publications, notably by Preece (2000, 2004). Among his many publications are three entitled "The Fungi of the Powysland District" (Vize 1892, 1894, 1896), and his downy mildew records from Montgomeryshire in the 1870s (Vize 1894, Francis & Waterhouse 1988) comprised the following 21 different species (applying modern taxonomy). These are the earliest extensive

downy mildew records from Wales (but see the account of Peronospora oerteliana below).

The following seventeen species were from Forden:

Bremia lactucae s.s. on Lactuca sativa Garden Lettuce

Bremia lapsanae on Lapsana communis Nipplewort

Bremia tulasnei on Senecio vulgaris Groundsel

Hyaloperonospora niessleana on Alliaria petiolata Garlic Mustard

Hyaloperonospora brassicae on Brassica oleracea Brussels Sprout

Peronospora aparines on Galium aparine Cleavers

Peronospora effusa on Spinacia oleracea Spinach

Peronospora ficariae on Ficaria verna Lesser Celandine

Peronospora grisea on Veronica beccabunga Brooklime

Peronospora lamii on Lamium maculatum Spotted Dead-nettle

Peronospora orteliana on Primula vulgaris Primrose

Peronospora pisi on Lathyrus oleraceus Garden Pea

Peronospora romanica on Medicago lupulina Black Medick

Peronospora violae on Viola sp. Violet

Plasmopara densa on Odontitites vernus Red Bartsia and Rhinanthus sp. Yellow-rattle

Plasmopara saniculae on Sanicula europaea Sanicle

Plasmoverna pygmaea on Anemone nemorosa Wood Anemone

Two were from nearby Berriew:

Peronospora arenariae on Moehringia trinervia Three-nerved Sandwort Pseudoperonospora urticae on Urtica dioica Common Nettle

One was from Montgomery:

Peronospora sordida on Scrophularia sp. Figwort

And one from Welshpool:

Peronospora calotheca on Galium odoratum Woodruff

P. saniculae has not been recorded from Wales since. Vize (1879) wrote: "To show how easy it is to meet with plants not recorded hitherto as British, I may name that, in my own

garden, within a few yards of the house" *Peronospora violae* and *P. lamii* were first found, and *P. calotheca* "was also first noticed in our country in Lord Powis's property at Welshpool."

More recently the only published regional mycota from Wales is that of Charles Aron who in 2005 produced his *Fungi of Northwest Wales*. He lists with their hosts two species of the Albuginaceae and 25 of the Peronosporaceae with 10km grid square distributional data and some detailed locality information within the vice-counties of Merionethshire, Caernarvonshire and Anglesey.

Dr. Tom F. Preece, in his *A checklist of the downy mildews (Peronosporaceae) of the British Isles*, published by the British Mycological Society in 2002, provides an invaluable listing of

mildew species, their hosts and the vice-counties (or sometimes broader counties) in Britain and Ireland from which records have been made. It is inevitably now taxonomically out of date, but the taxonomy has been updated here in extracting the records.

On his retirement from the University of Leeds, Tom (pictured right) moved close to the Welsh border near Oswestry and contributed much to our knowledge of plant pathogens in this area, assisting colleagues In Wales in the recording and identification of selected fungal and downy mildew pathogen species.



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Following the Census Catalogue below we provide a tabulation of host genera and the mildews they have been found to support in Britain and Ireland. It is included as a guide to what has been recorded and should not be used for making reliable determinations, nor does it pretend to be an accurate checklist for Britain and Ireland. It is essentially a summary of our records for Wales and an attempt at an interpretation and update of the invaluable records in the Fungal Records Database of Britain and Ireland (FRDBI) of the British Mycological Society, those in Preece (2002) and those by various other authors and recorders for the rest of Britain and Ireland. In all cases the species accounts below should be consulted before making an identification.

Indications of wider distributions in Britain and Ireland in the species accounts below are mostly taken from the FRDBI and Preece (2002) but are of necessity very approximate. The lack of expected records of many mildews of horticultural and agricultural species is doubtless at least partly because such records are no longer being collected by official bodies as they used to be. Entries for a few genera and species of special interest or relevance recorded elsewhere in Britain but not in Wales are given in square brackets.

Following the species accounts, to summarize what is known of the distribution of these organisms in Wales a census catalogue, assigning the records alphabetically by both mildews and hosts that we have been able to trace to each of the thirteen vice-counties (Watson, 1883) is presented below. The box below provides a list of Welsh vice-counties and their abbreviations and numbers as used in the species accounts and census catalogue. Further details and a brief analysis of records are provided in the introduction to the census catalogue.

Vice-county abbreviations and numbers:

35	Monmouthshire Mons	47	Montgomeryshire Monts
41	Glamorgan Glam	48	Merionethshire Mer
42	Breconshire Brecs	49	Caernarvonshire Caerns
43	Radnorshire Rads	50	Denbighshire Denbs
44	Carmarthenshire Carms	51	Flintshire Flints
45	Pembrokeshire Pembs	52	Anglesey Angl
46	Cardiganshire Cards		

Species Accounts

The species accounts below through illustrations, where available, and descriptions seek to assist the finding and identification of Welsh downy mildews and white blister-rusts. Genera are arranged alphabetically within families as are species within genera. The Peronosporaceae are considered first followed by the Albuginaceae. To complete a picture of the diversity of these organisms in Britain we have included within square brackets descriptions of genera found in Britain but yet to be recorded from Wales and a selection of species most likely to occur in Wales but which have yet to be detected. Records referred to as "old" were made pre 1970. Where the wider distribution is given as Britain, it can be assumed that records have been traced for both Scotland and England; where records have been reported from Ireland, they may be from Northern Ireland, Eire or both. At the end of each species account, where data is available for Wales, a tentative indication is given as to when in the year records have been made. It is hoped this will help the rediscovery of old records and facilitate the discovery of new sites.

Peronosporaceae

Sporangiophores are long and branched above, forming downy or felt-like colonies. The sporangia produce germ tubes in some genera and zoospores in others. Eight genera and 123 taxa have been recorded from Wales. Most host species support only a single downy mildew species. In Wales the only hosts supporting multiple species are *Cerastium fontanum* Common Mouse-ear with *Peronospora conferta* and *P. paula*, *C. glomeratum* Sticky Mouse-ear with these two plus *P. tomentosa*, and possibly *Ranunculus acris* Meadow Buttercup with *P. hiemalis* and *P. ranunculi*. Where the host supports more than one species, we indicate diagnostic characters.

[Basidiophora de Bary

Parasitic on Asteraceae Daisy family. Not yet recorded in Wales, and in Britain recorded only once, when *B. entospora* Roze & Cornu was found on *Erigeron canadensis* Canadian Fleabane at Wimbledon, Surrey in 1867. The haustoria are vesicular. The colonies are white or greyish, and the sporangiophores are unbranched except at the very narrowly clubshaped apex where there are 8-25 short projections bearing the sporangia (see Constantinescu 1998).]

Bremia Regel

Parasitic on Asteraceae Daisy family. Haustoria are vesicular, often pyriform. Colonies are whitish and not very dense. Sporangiophores are dichotomously branched at 45° or more, swollen at the apex and disclike, with three to five points from which the sporangia develop. Sporangia germinate to produce a germ tube. Eight taxa are recorded from Wales.

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Bremia centaureae Syd. s.l. (B. lactucae s.l.)

Bremia sp. sporangiophore Confined to Centaurea Knapweeds, and recorded on C. nigra Common Knapweed twice in Cards and Caerns and once each in Carms and Mer. Colonies are whitish and cause yellowish patches above. Recorded throughout Britain and Ireland. May-Nov.



Bremia centaureae on Centaurea nigra

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Bremia cirsii (Jacz. ex Uljan) J.F. Tao & Y.N. Yu (B. lactucae s.l.)

Confined to Cirsium Thistles and recorded on C. palustre Marsh Thistle in Caerns, and on C. vulgare Spear Thistle in Rads, Cards, Caerns and Angl. Colonies are whitish, and cause yellowish patches above and some slight distortion. Recorded throughout Britain. All year.

Bremia lactucae Regel s.l.

Parasitic on a wide range of genera of the Asteraceae, Daisy family. Choi & Thines (2015) show that some of the proposed taxonomic splits are justified and we adopt them here. The group is likely soon to be further split up. Colonies are white as in B. lactucae s.s., with pale patches above and usually causing slight deformity of the host. In Wales the only records





Bremia cirsii on Cirsium palustre

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that cannot yet be assigned further are ones on *Hieracium* sp. Hawkweed and *Crepis capillaris* Smooth Hawk's-beard in Caerns and on *Pilosella aurantiaca* Fox-and-cubs in Rads, Cards and Caerns. There are scattered records throughout Britain and Ireland on various genera (see Legon & Spooner 2015). Apr-Dec.



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Bremia lactucae s.l. on Pilosella aurantiaca

Bremia lactucae Regel s.s.

Confined in the strict sense to *Lactuca* Lettuces, and frequently recorded in the past and less often recently from most vice-counties in Wales on *L. sativa* Garden Lettuce in cultivation (whether this indicates a decline in occurrence, the growing of more resistant varieties, or in the keeping of records is uncertain). The colonies on the lower surface of the leaves are white, causing pale yellowish-green patches above, and sometimes some distortion, leading to necrosis. Commonly recorded throughout Britain and Ireland where it can be a commercially significant pest. Seasonality unknown in Wales.

Bremia lapsanae Syd. (B. lactucae s.l.)

Confined to *Lapsana* Nippleworts and recorded on *L. communis* Nipplewort in Brecs, Rads, Cards, Carms, Denbs and Flints, with an old record in Monts. Colonies are whitish and cause pale yellowish patches above and very slight distortion. The rather dense whitish



Bremia lactucae s.s. on Lactuca sativa



Bremia lapsanae on Lapsana communis

sporangiophores when young, even under a lens, may be easily mistaken for *Ramularia lampsanae* and should be checked under the microscope. The clumped conidiophores of the *Ramularia* are unbranched, whilst even when young, the *Bremia* sporangiophores are richly branched. Note also that the disc-like tips only develop when the sporangiophores mature. Recorded throughout Britain and Ireland. All year.

Bremia sonchicola (Schltdl.) L. Ling & M.C. Tai (*B. stellata* (Desm.) Kochman & T. Majewski, *B. lactucae* s.l.)

Confined to *Sonchus* Sowthistles and rarely recorded in Wales. Noted on *Sonchus asper* Prickly Sowthistle in Mons, Brecs, Cards, Monts, Caerns and Angl with an old record from Rads, and on *S. oleraceus* Smooth Sowthistle in Rads and Caerns. Colonies are whitish and cause pale spots on the lower surface of the leaf and yellowish patches above, with little or no distortion. They can also occasionally distort the leaves. It has been widely recorded throughout Britain and Ireland as *B. lactucae*. May-Aug.



Bremia sonchicola on Sonchus oleraceus

Bremia sonchicola on Sonchus asper

Bremia taraxaci S. Ito & Tokun. (*B. lactucae* s.l.)

Confined to *Taraxacum* Dandelions, and recorded in Wales only on an unidentified species of the genus in Cards. Colonies are whitish and cause yellowish patches above and little or no distortion. There are scattered records throughout Britain. Oct.

Bremia taraxaci sporangiophores (right)



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Bremia tulasnei (Hoffm.) Syd. (B. lactucae s.l.)

Confined to *Jacobaea* Ragworts, *Senecio* Ragworts, *Pericallis* Cinerarias, *Xerochrysum* Strawflowers and other related genera. In Wales it has been recorded only on *Jacobaea vulgaris* Common Ragwort in Carms and Caerns, and on *Senecio vulgaris* Groundsel in Rads (where it occurred twice on the same leaves as *Pustula obtusata* s.l.) and Caerns, with

old records in Monts and Mer. Colonies are whitish and can cause yellowish patches above and sometimes slight distortion.
Recorded throughout Britain and Ireland. All year.

Bremia tulasnei with scattered discrete white sporangiophores amongst the cream-coloured sori of Pustula obtusata on a leaf of Senecio vulgaris (right).



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Hyaloperonospora Constant.

The species of *Hyaloperonospora* (formerly included in Peronospora) on hosts in the Brassicaceae Cabbage family and related families were formerly called *H. parasitica*, but are now mostly assigned to other species. The genus is confined to Brassicaceae in Britain. Haustoria in the host tissue are vesicular, entire or lobed. Colonies are predominantly white and dense. Sporangiophores are monopodially branched (at least the primary branching), with primary branching at 45° or more, the ultimate branches usually strongly recurved with their apices pointed (see image right). Sporangia germinate to produce a germ tube. There is much valuable information on the genus in Constantinescu & Fatehi (2002) and Göker et al. (2009). Sixteen taxa are recorded from Wales.



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Hyaloperonospora arabidopsidis (Gäum.) Göker, Riethm., M. Weiss & Oberw. (*H. parasitica* s.l.)

Confined to *Arabidopsis* Thale Cresses and found twice in Wales on *A. thaliana* Thale Cress, on both occasions in churchyards, with records from St. Dingat's, Llandovery, Carms and Llanbadarn Fawr, Cards. The whitish colonies caused some leaf deformity and created pale patches above on the leaves, but on both specimens found, it did not inhibit development of the inflorescence, contrary to what Klenke & Scholler (2015) suggest. It has been recorded sparingly in England as *H. parasitica*. All year.



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Hyaloperonospora arabidopsis with diffuse sporangiophores and the white blisters of Albugo candida s.l. on an Arabidopsis thaliana leaf.

Hyaloperonospora barbareae (Gäum.) Göker, Riethm., M. Weiss & Oberw.(H. parasitica s.l.)

Recorded twice in Wales, on *Barbarea verna* American Winter-cress at the Ynys-las boatyard in Cards and in a car park at Groeslon, Caerns. It is confined to *Barbarea*, and apparently has not been recorded elsewhere in Britain. The greyish-white colonies cause pale orange-brown patches above without distorting the leaves. Apr-May.

Hyaloperonospora barbareae on Barbarea verna (right)

Hyaloperonospora brassicae (Gäum.) Göker, Voglmayr, Riethm., M. Weiss & Oberw. (*H. parasitica* s.l.)



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Confined chiefly to Brassica Cabbages,

Armoracia Horse-radishes, Raphanus Radishes, and Sinapis Mustards, and widely recorded in Wales on cultivated Brassica, chiefly in the past, usually as H. parasitica. The recent record from Denbs on B. napus and old records from Mons, Cards and Caerns could be on either Oil-seed Rape or more probably Swedes. Similarly, recent records from Mons and Denbs and old records from Glam, Monts and Flints on Brassica oleracea cannot be ascribed to a ssp. of cabbage. There are also records on Sinapis arvensis Charlock and on B. rapa ssp. campestris Wild Turnip from Henfaes, Aber, Caerns. On Brassica oleracea var. viridis Curly Kale in a garden in Aberystwyth, Cards in 2019 a few sporangiophores were

seen at the edge of an *Albugo candida* s.l. blister. The greyish-white colonies produce pale brownish patches on the leaves (and often blisters where the oogonia form), and seedlings are often killed. Recorded throughout Britain and Ireland on all four of these genera. June-Dec.



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Hyaloperonospora brassicae on Sinapis arvensis (see also overleaf)

Hyaloperonospora camelinae (Gäum.) Göker, Voglmayr, Riethm. & Oberw.(H. parasitica s.l.)

Confined to *Camelina* Gold-of-pleasures, and recorded once in Wales in a crop of *C. microcarpa* Lesser Gold-of-pleasure at Bethel in Caerns in 2006 (see image overleaf). Yellowish-white colonies on the leaves have pale green or yellowish spots above, and they can also occur on the stems causing distortion, the infection probably being systemic. There seem to be no other records from Britain. July.



Hyaloperonospora brassicae on Brassica sp. (above)

Hyaloperonospora camelinae on Camelina microcarpa (right)

Hyaloperonospora cheiranthi Göker, Riethm., M. Weiss & Oberw. (H. parasitica s.l.)

Confined to Erysimum spp. Wallflowers and recorded in Wales and Britain only on Erysimum cheiri Wallflower, with records in Wales from Rads, Cards and Caerns. Infected leaves develop pale yellow patches above, curl and become brownish and necrotic. There are scattered records throughout England and Ireland on this host. Mar-May.





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Hyaloperonospora cheiranthi on Erysimum cheiri

Hyaloperonospora cochleariae on Cochlearia danica

Hyaloperonospora cochleariae (Gäum.) Göker, Voglmayr, Riethm., M. Weiss & Oberw. (*H. parasitica* s.l.)

Recorded only twice in Britain, on *Cochlearia officinalis* Common Scurvygrass on the sea cliffs at Borth in Cards in 2012 and on *C. danica* Danish Scurvygrass on Rhosneigr beach, Angl in 2009. The greyish-white colonies are inconspicuous and cause slight paleness above. Probably confined to *Cochlearia* Scurvygrasses. It was reported on *Armoracia sativa* Horse-radish by Klenke & Scholler (2015), but on this host Göker *et al.* (2009) show it to be *H. brassicae*. March.

[Hyaloperonospora dentariae (Rabenh.) Voglmayr see H. nasturtii-aquatici below].

Hyaloperonospora erucastri (Gäum.) Choi & Thines (H. parasitica s.l.)

Confined to *Erucastrum* Hairy Rockets and *Hirschfeldia* spp. Hoary Mustards, it has been collected in Wales only on *Hirschfeldia incana* Hoary Mustard from a trackside at Llan-non in Cards. The colonies are greyish-white and rather sparse, with obscure, pale patches above (see image below), and the sporangia have a mean diameter of 20 × 17µm. It seems not to have been recorded in Britain before. According to W.N. Ellis, Plant Parasites of Europe website (2017) "The reference by Klenke & Scholler (2015) to *Hirschfeldia incana* probably concerns a different, possibly as yet undescribed *Hyaloperonospora*." July.



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Hyaloperonospora erucastri on Hirschfeldia incana

Hyaloperonospora galligena (S. Blumer) Göker, Riethm., Voglmayr, M. Weiss & Oberw. (*H. parasitica* s.l.)

Confined to *Alyssoides* Alisons and *Aurinia* Golden Alisons. It has been recorded from Glam in 1955 and Flints in 1978 on *Aurinia saxatilis* Golden Alison. The white colonies form on small swellings on the leaves, stems and inflorescences, causing some distortion. Widely recorded on this host throughout Britain. Sept.

Hyaloperonospora hesperidis (Gäum.) Göker, Riethm., Voglmayr, M. Weiss & Oberw. (*H. parasitica* s.l.).

Confined to *Hesperis* Dame's-violets and recorded in Wales only on *H. matronalis* Dame's-violet in a garden near Llysdinam in Brecs in 2019 (although it had been seen here for many



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Hyaloperonospora hesperidis on Hesperis matronalis

years unidentified). Greyish-white colonies on both surfaces of the leaves cause brown, darkly outlined mottling. Heavily infected plants become yellow-brown with the leaves held in a more upright position than normal. Recorded in Britain otherwise only from Yorkshire and Orkney. March-June.

Hyaloperonospora hesperidis on Hesperis matronalis (right)

Hyaloperonospora lobulariae (Ubrizsy & Vörös) Göker, Voglmayr & Oberw.(*H. parasitica* s.l.)

Confined to *Lobularia* Sweet Alisons and recorded only twice in Wales from Neath in Glam in 1997 and from a garden at Felinheli, Caerns in 2006, on *Lobularia maritima* Sweet Alison. The greyish-white colonies cause brownish-violet patches above and,



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unlike *Albugo candida* s.l. on this host, cause no distortion to the leaves. Otherwise in Britain it has been recorded only a few times in England. Aug-Sept.

Hyaloperonospora nasturtii-aquatici (Gäum.) Voglmayr (H. parasitica s.l.)

This species occurs only on *Cardamine* Bitter-cresses and *Nasturtium* Water-cresses. It has been recorded on *Cardamine flexuosa* Wavy Bitter-cress in Glam, Brecs, Rads, Carms,



Hyaloperonospora nasturtii-aquatici on Cardamine flexuosa



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Hyaloperonospora nasturtii-aquatici and Albugo candida s.l. on Cardamine flexuosa

Cards and Caerns; and on *C. hirsuta* Hairy Bitter-cress in Mons, Brecs, Rads, Carms, Pembs and Cards and on these two hosts it often occurs with the white blister-rust Albugo candida s.l. Also recorded on C. pratensis Cuckooflower in Carms and on Nasturtium officinale Water-cress in Brecs. The mildew occurs mostly on the older basal leaves, which turn yellowish, with the grey colonies forming on the lower leaf surface. On a road verge at Llanelli, Glam and in a churchyard at Llandefaelog, Brecs, both in 2019, it was associated with the blisters of Albugo candida s.l. on Cardamine flexuosa. It has been recorded throughout Britain and Ireland on Cardamine spp., and once from Yorkshire on Nasturtium

sp. March-Dec. Hyaloperonospora dentariae (Rabenh.) Voglmayr, not yet recorded in Wales, is confined to several other species of Cardamine (see Voglmayr et al. (2014)) and has been recorded several times in the south of England on C. bulbifera Coralroot. Of its possible hosts the only one in Wales is C. impatiens Narrow-leaved Bitter-cress on which it should be sought.

Hyaloperonospora niessliana (Berl.) Constant. (H. parasitica s.l.)

Confined to Alliaria petiolata Garlic Mustard and very common throughout Wales, particularly on roadside banks and verges where the host is most frequently seen. The colonies are well-defined and often angular and vein-delimited, dense and very white,



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Hyaloperonospora niessliana on Alliaria petiolata

and usually on the lower surface of the leaf. They cause pale patches above but with no significant distortion of the leaf. It is commonly recorded throughout most of the rest of Britain and Ireland. March-Nov.

[Hyaloperonospora parasitica s.l.

Records from Wales previously given as *H. parasitica* or *Peronospora parasitica* have now mostly been reassigned as indicated, except for those on *Capsella* Shepherd's-purses and *Crambe* Sea-kales.]

Hyaloperonospora parasitica (Pers.) Constant. s.s.

In the strict sense, *H. parasitica* is probably confined to Capsella in Wales. It has been recorded on Capsella bursa-pastoris Shepherd's-purse from Brecs, Carms, Cards and Caerns, and in 1933 on Crambe maritima Sea-kale in Glam, and widely throughout Britain and Ireland. The white colonies can occur all over the host causing considerable distortion. At one site in Cards in 2010, a fallow field at IBERS, Plas Gogerddan, Cards, it was associated with the blisters of Albugo candida s.s. on Capsella bursa-pastoris. It was this close and common association that led to the choice of the mildew's specific name of "parasitica" since it was thought, incorrectly, to be a parasite of Albugo. Apr-Oct.



Hyaloperonospora parasitica on Capsella bursa-pastoris



Hyaloperonospora praecox Voglmayr & Göker

Unusually, two species of Hyaloperonospora are recorded on Erophila spp. Whitlowgrasses. Only H. praecox has been found in Wales, on Erophila verna Common Whitlowgrass as a pavement weed in Newtown, Monts. The white colonies on the lower surface of the leaves cause discolouration above. but no distortion, unlike H. erophilae (Gäum.) Göker, Voglmayr, Reithm., Weiss & Oberw. which is systemic, distorting the whole plant and inhibiting flowering (Voglmayr



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Hyaloperonospora praecox on Erophila verna

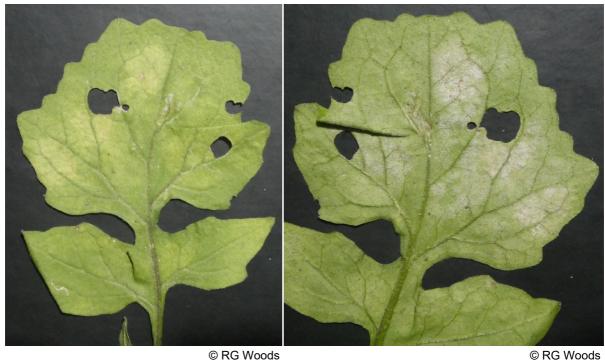
& Göker 2011). The latter has not been recorded in Wales, but is known from the Outer Hebrides and is doubtless elsewhere in Britain. *H. praecox* is recorded elsewhere from Cambridgeshire, and is also probably more widespread. Apr.

Hyaloperonospora rorippae-islandicae (Gäum.) Göker, Voglmayr, & Oberw. (*H. parasitica* s.l.)

Confined to *Rorippa* Yellow-cresses and recorded on *R. islandica* Northern Yellow-cress from Brecs and Cards, and *R. palustris* Marsh Yellow-cress from Brecs, with an old record from Cards. It is recorded on *R. palustris* and *R. sylvestris* Creeping Yellow-cress from a few sites in England. Based on Korean material, Lee *et al.* (2017) recognized a separate species on *R. palustris* as *Hyaloperonospora nasturtii-palustris* (Gäum.) J.S. Lee & Y.-J. Choi, differing morphologically in its sporangia averaging $18.5 \times 14.1 \mu m$, while those of *H. rorippae-islandicae* average $16.6 \times 13.8 \mu m$. Whether both species occur in Britain is not yet known. Material on *R. palustris* from Llangorse Lake in Brecs had sporangia varying greatly from $15 \times 13 \mu m$ to $20 \times 18 \mu m$, averaging $17.1 \times 14.7 \mu m$ (n=15). Aug.

Hyaloperonospora sisymbrii-loeselii (Gäum.) Göker, Riethm., Voglmayr, M. Weiss & Oberw. (*H. parasitica* s.l.)

Probably confined to *Sisymbrium* Rockets, it has been recorded on *Sisymbrium officinale* Hedge Mustard from several vice-counties in Wales. Slight yellowing of the upper leaf surfaces betrays the presence of the distinctive white colonies on the lower leaf surface. Recorded on this and other species in the genus throughout England. Apr-Nov.

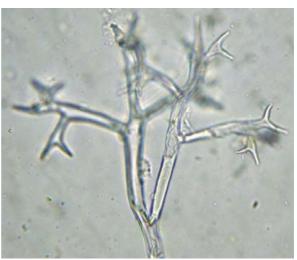


Hyaloperonospora sisymbrii-loeselii on Sisymbrium officinale

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Paraperonospora Constant.

Parasitic on Asteraceae, chiefly in the tribe Anthemideae. Haustoria are vesicular, often pyriform and are entire. Colonies are white. Sporangiophores (see image right) tend to be dichotomously or sometimes trichotomously branched, with the main branches variably angled and more or less widened towards the apex. Apices of the sporangiophores are truncate, rounded or swollen. The sporangia produce a germ tube. Much useful additional information can be found in Constantinescu (1989).



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Paraperonospora leptosperma (de Bary) Constant. s.l.

Found on many genera within the Anthemideae in the Asteraceae Daisy family. Small, patchy yellowing of parts of the finely divided leaves may betray the presence of this mildew. A careful search with a lens will confirm the presence of scattered sporangiophores. Occasionally the colonies on Matricaria discoidea Pineappleweed as in the image below right taken at the edge of a Potato field, near Burfa, Rads in 2019 may be conspicuous. This species has only been found on this host elsewhere in Wales in an Oat crop at Monachty, Cards in 2013. There are also recent records on M. chamomilla Scented Mayweed as a field weed near Clyro, Rads, at Henfaes, Aber, Caerns and at Valley, Angl; on Tripleurospermum



Paraperonospora leptosperma on Matricaria discoidea

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© AO Chater Paraperonospora leptosperma on Tripleurospermum maritimum

© AO Chater

maritimum subsp. maritimum Sea Mayweed on the Ynys-las dunes in 2013 and in a caravan park at Clarach in 2015, both in Cards, and in two places beside the Wales Coastal Path at Four Mile Bridge and Cemlyn on Angl, and on *T. inodorum* Scentless Mayweed at the edge of a Barley crop at Llan-non in Cards in 2019. There are scattered records on these and other species in these two genera, and on *Anthemis* Chamomiles throughout Britain and Ireland. Further work will doubtess recognise several new segregates. May-July.

Perofascia Constant.

Parasitic on *Lepidium* Pepperworts. Haustoria are hypha-like and branched. Colonies are whitish. Sporangiophores are mostly dichotomously branched, the primary branches very strict or almost parallel, at less than 45° (see image below right). Many or even most sporangia are pointed or apiculate (see image below left). The sporangia produce zoospores. Much useful additional information can be found in Constantinescu & Fatehi (2002). According to them the sporangiophore branching is "basically monopodial but appearing anisotomously dichotomous" [ie with the two branches of a pair differing in size], but in our experience in the great majority of cases it appears straightforwardly dichotomous.



Perofascia sporangia (left) and sporangiophore (right)

Perofascia lepidii (McAlpine) Constant.

Confined to *Lepidium* Pepperworts and recorded in Wales only on *L. coronopus* Swine-cress and *L. didymum* Lesser Swine-cress at a few sites in Cards. The colonies are greyish-white and fairly sparse with the infected parts of the leaves and stems yellowish, and usually

slightly distorted and dwarfed. Later in the season infection can be largely confined to the fruits. Recorded in England north to Lincolnshire. Apr-Oct.



Perofascia lepidii on Lepidium coronopus

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Peronospora Corda

Parasitic on a wide range of plants.
Haustoria are hypha-like and branched.
Colonies are pale to dark greyish-white or violet-tinged. Sporangiophores monopodially branched (but can appear more or less dichotomously so), with primary branches at 45° or more). Apices of the sporangiophores are pointed. The sporangia on germinating produce a germ tube. Eighty taxa have been recorded from Wales.

Peronospora fulva sporangiophore



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Peronospora aestivalis Syd. s.l.

Confined to *Medicago* Medicks and recorded on *M. sativa* ssp. *sativa* Lucerne from Glam in 1939 and 1940 and in Pembrey Forest in Carms in 1994 (as *P. trifoliorum*), and widely in England on this host. Colonies are brownish-violet-tinged, often with yellowish discolouration above, and can cause deformation on young plants. The sporangia are larger (av. 27 × $20\mu m$) and the oospores smaller (av. <35 μm) than those of *P. romanica* on *M. lupulina* Black Medick (av.20 × $17\mu m$ and >35 μm).

Peronospora affinis Rossmann

Confined to *Fumaria* Fumitories and recorded on *F. muralis* subsp. *boraei* Common Ramping-fumitory from five sites in Cards, two in Brecs, three in Rads, one in Pembs and



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Peronospora affinis on Fumaria muralis ssp. boraei



Peronospora affinis on Fumaria muralis ssp. boraei

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Peronospora affinis on Fumaria muralis ssp. boraei

Caerns and two in Denbs, on *Fumaria bastardii* var. *bastardii* Tall Ramping-fumitory from one site in Pembs, three in Cards and two in Caerns, on *F. officinalis* subsp. *officinalis* Common Fumitory from one site Carms and Cards, and once on subsp. *wirtgenii* in Cards, twice on *F. officinalis* s.l. in Carms, and once each in Rads, Pembs, Caerns and Angl. It is doubtless more widespread but overlooked. The colonies are dull violet-tinged and the

infected leaves are pale and usually distorted, but often only parts of the leaves are infected. Widely recorded in Britain and Ireland. All year.

Peronospora agrestis Gäum.

Confined to Veronica Speedwells, it has, in Wales, been recorded once on Veronica agrestis Green Field-speedwell in a garden in Rads, four times on Veronica arvensis Wall Speedwell along the coast in Cards, and in an Oil-seed Rape field and in Sheep-grazed turf on a common, both in Rads; twice on V. persica Common Field-speedwell on a roadside verge in Pembs and in an arable field in Caerns; once on V. chamaedrys Germander Speedwell on a



Peronospora agrestis on Veronica persica



Peronospora agrestis on Veronica arvensis

roadside bank at Glandyfi in Cards; and once on *V. filiformis* Slender Speedwell in Glam. Initial infection turns the plant yellow. The colonies on the lower surface of the leaves are greyish, and the infected leaves finally turn brownish and wither early, most noticeably in *V. agrestis*. Infection can start very early on the first pair of leaves above the cotyledons of seedlings. Widely recorded throughout Britain and Ireland on these species and on *V. polita* Grey Field-speedwell. All year.

Peronospora agrimoniae Syd.

A tiny amount was discovered on the leaf of an *Agrimonia* sp. in a large population of mixed *A. eupatoria* Agrimony and *A. procera* Fragrant Agrimony on a trackside verge near Cwmbach Llechrhyd, Rads in 2019. This is possibly the first British record for this taxon, confined to *Agrimonia* Agrimonies, that is known from several sites in Germany and the Czech Republic (Petrželová *et al.* 2017). The upper leaf surface shows vein-delimited yellowing between the veins with purple mottling. The colonies on the lower surface are indistinct, being hidden between the many hairs on the leaf. The sporangia are c.15µm in diameter. The plant was not flowering and the leaf could not be confidently ascribed to a particular host species. June.



© RG Woods Peronospora agrimoniae on Agrimonia sp.

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Peronospora alsinearum Casp.

Confined to Stellaria Stitchworts with scattered recent records in Wales on S. media, Common Chickweed in Carms, Pembs, Cards, Caerns and Angl, with an old record from Monts. It has been recorded throughout Britain and Ireland. The colonies are greyish-white and infected leaves and stems are pale and sometimes etiolated and thickened. Oospores and sporangiophores can be abundant even as early as on the cotyledons of seedlings, and oospores are also usually abundant in the sepals, petals and ovaries. Peronospora parva also occurs on Stellaria in Wales, and has smaller sporangia, averaging 19 × 16µm as against 27 × 22µm. Dec-July.



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Peronospora alsinearum on Stellaria media



Oospores of Peronospora alsinearum in the sepals of Stellaria media

Peronospora alta Fuckel

Confined to *Plantago* Plantains, and recorded widely throughout Wales, but surprisingly rare in some areas (only two records in Cards) as well as throughout Britain and Ireland, on *P. major* Greater Plantain. On *P. lanceolata* Ribwort Plantain there is one old record from Flints, and only a few elsewhere in Britain. Infected plants can be conspicuous since the greyish colonies on the lower surface of the leaf cause pale yellowish patches above. Occasionally whole leaves may be infected creating a greyish caste to the upper surface, but the symptoms on *P. lanceolata* are said to be less obvious than on *P. major* (Gustavsson 1991). May-Sept.



© RG Woods

Peronospora alta on Plantago major

Peronospora anemones Tramier

Recorded on the cultivated *Anemone coronaria* Poppy Anemone, its only host, from four vice-counties in Wales, but not in the last 50 years. Morphologically it is almost identical to *P. ficariae*. Colonies are greyish-white, making the leaves greyish and with purplish necrotic areas, and are often slightly distorted and downcurved. Sparingly recorded in England, mostly in the south. Nov.

Peronospora antirrhini J. Schröt.

Confined to Antirrhinum Snapdragons and Misopates Weasel's-snouts in the Veronicaceae Speedwell family. Moore (1959) notes that the second British record of this species unknown in the British Isles before 1936, was from Aberystwyth, Cards in 1940. Recorded on Antirrhinum majus Snapdragon from four Welsh vice-counties, but not in the last 50 years, though widely recorded on this host throughout Britain and from Ireland. On Misopates orontium Weasel's-snout it was recorded at Felinfoel in Carms in 1997, and there are a few records on this host from England and Scotland. Infected plants are dwarfed and etiolated, the pale greyish-violet colonies on the lower leaf surface causing yellowish or reddish colouration above. Sept.

Peronospora aparines (de Bary) Gäum.

Common on, and confined to Galium aparine Cleavers, appearing on the seedlings in winter or early spring, and often persisting on old plants until the following winter. Infected shoots and leaves are conspicuously pale or yellowish and often etiolated. The colonies are greyish or violet-tinged on the undersurface of the leaves. Recorded from most Welsh vice-counties, doubtless present in all, and commonly recorded throughout Britain and Ireland. All year.



Peronospora aparines on Galium aparine

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Peronospora arborescens (Berk) Casp. s.l.

The long-standing confusion in the taxonomy of *Peronospora* on *Papaver* Poppies and Meconopsis Blue Poppies was partly resolved by Voglmayr et al. (2014). Peronospora arborescens, with smooth oospore walls and sporangia averaging <20µm, was confined by them among the species they considered (some annuals plus Papaver cambricum Welsh Poppy) to Papaver rhoeas Corn Poppy. As such, it has not been recorded on this species in Wales, and records of Peronospora arborescens on Papaver cambricum and P. somniferum Opium Poppy are referable to *Peronospora meconopsidis*. Material previously referable to *P.* arborescens and not yet assigned to a definite species by Voglmayr et al. (2014) has,



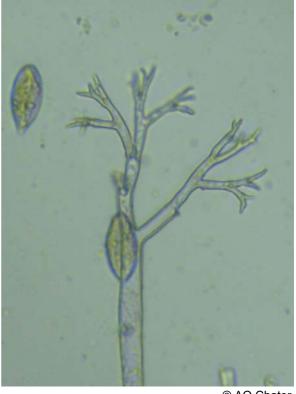
© DA Evans Peronospora arborescens s.l. on Papver dubium

© DA Evans

however been recorded twice in Wales. On *Papaver setiferum* Oriental Poppy in the walled garden, Llanerchaeron, Cards, the sporangia averaged 19.2 × 18.4µm (see image right of sporangia). The colonies were brownish and covered most of the infected leaf lobes, which were brownish above. Oospores were not found. On *P. dubium* Long-headed Poppy it was found on disturbed ground at Tregele, Angl in 2019. May.

Peronospora arenariae (Berk.) Tul.

Confined to *Moehringia* Three-nerved Sandworts, there are single records from Carms and Flints, and three from Cards, as well as an 1870s Vize record from Monts, on *M. trinervia* Three-nerved Sandwort. The colonies are greyish, and as *P. arenariae* is fairly conspicuous and etiolates or distorts



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the leaves and shoots, it is unlikely to have been much overlooked. There are scattered records throughout Britain. Apr-May.

Peronospora arvensis Gäum.

Confined to *Veronica hederifolia* lvy-leaved Speedwell. This species is very common especially along hedgebanks and road verges in spring where it appears from late January on seedlings and has usually gone by the end of May. Recorded from nine Welsh vice-

counties, but doubtless present in all. Colonies on the leaf undersurface are greyish-white, and cause the leaves to become brownish or pale and sometimes slightly etiolated. Widely recorded in England and Wales, mostly in the south. Jan-Aug.

Peronospora arvensis on Veronica hederifolia (right)

Peronospora boni-henrici Gäum. (P. farinosa s.l.)

Confined to *Blitum bonus-henricus* Good-King-Henry and recorded from Mons and Angl, with scattered records from England. Colonies are brownish-violet, quite dark and often cover the whole lower surface of the leaf and cause large yellowish or brownish patches, or colour the whole leaf, above.



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© DA Evans Peronospora boni-henrici on Blitum bonus-henricus

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Peronospora calotheca Fuckel

Confined to *Galium odoratum* Woodruff and *Asperula* Woodruffs. Recorded recently on *Galium odoratum* from seven Welsh vice-counties and widely reported elsewhere in Britain and Ireland. In Wales it is, however, far from common. The greyish colonies are on the lower leaf surface, and infected leaves become yellowish usually from the base, then conspicuously reddish-bronze and blackish as they die. Infected *G. odoratum* colonies may be conspicuous as the upper whorls of leaves are often the most heavily infected and many stems in a colony may be infected. Most records are from moist ancient woodlands where the host is presumably native. The single Rads record is in a garden close to an ancient woodland site with this mildew and in Denbs it is recorded from a churchyard with woodland some distance away. May-July.

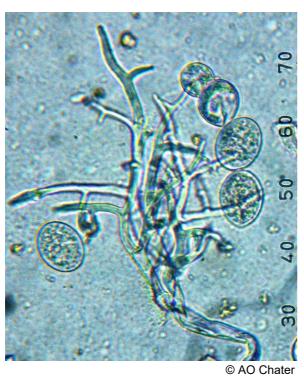




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Peronospora calotheca on Galium odoratum



Peronospora calotheca sporangiophores

Peronospora chenopodii Schltdl. (*P. farinosa* s.l.)

Confined to Chenopodium s.l., Goosefoots. There are several records on *Chenopodium* album Fat-hen from Brecs, Rads, Carms, Pembs, Cards, Caerns, Denbs, Flints and Angl, one record on C. ficifolium Fig-leaved Goosefoot from each of Carms and Cards, and one on Oxybasis rubrum Red Goosefoot from Mons. The colonies are greyish, causing conspicuous pale or yellowish spots or patches above. Commonly recorded throughout Britain and Ireland. Choi et al. (2008) suggest that the species on Chenopodium album is Peronospora variablis; this is however synonymized with Peronospora chenopodii by Klenke & Scholler (2015). In one Carms locality adjacent plants of C. album and C. filicifolium supported colonies of this mildew whilst in

Gloucestershire, England, in a large closely-mixed population of these two species with *Lipandra polyspermum* Many-seeded Goosefoot only the latter showed symptoms of infection, reinforcing the need to reinvestigate the host specificity of this downy mildew. May-Sept.



Peronospora chenopodii on Chenopodium filicifolium



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Peronospora chenopodii on Chenopodium album



© RG Woods

Peronospora chenopodii on Chenopodium album

[Peronospora chrysosplenii Fuckel

Confined to *Chrysosplenium* Goldensaxifrages, and recorded from a few sites in England and Scotland on both *C. alternifolium* Alternate-leaved Goldensaxifrage and *C. oppositifolium* Opposite-leaved Golden-saxifrage. As it has been recorded on the former on the Welsh border at Craig Sychtyn in Shropshire, as well as in several other counties in Britain, it should be looked for in Wales. Colonies are greyish, the infected leaves and shoot apices are enlarged, yellowish and pale and the leaf margins are often downcurved.]

Peronospora conferta (Unger) Unger

Confined to *Cerastium* Mouse-ears and much the commoner of the two species (the other being *P. paula*) on *C. fontanum* ssp. *vulgare* Common Mouse-ear. The mildew usually covers the whole lower surface of the leaf, or sometimes just a well-

demarcated part of the leaf, and causes the infected parts and often whole shoots to become yellowish and very conspicuous. It has been recorded from numerous sites in Cards and Angl and more sparingly in Brecs, Rads, Carms, Pembs, Monts, Caerns and Flints and



Peronospora conferta on Cerastium fontanum ssp. vulgare

© RG Woods



Peronospora conferta oospore

Peronospora conferta on Cerastium fontanum ssp. vulgare

is doubtless in all the Welsh vice-counties. A collection on *C. glomeratum* Sticky Mouse-ear from a dry grassy mound at Ynys-hir in Cards has the sporangia $22-29 \times 20-22\mu m$, subglobose to ellipsoid, and must be referable to *P. conferta*, but many other Cards specimens on this host, with the sporangia in the general range of $15-25 \times 12-19\mu m$, are possibly *P. conferta*, or possibly *P. tomentosa* (the usual species on *C. glomeratum*) whose

upper limit is usually given as $22 \times 17 \mu m$. A Carms collection on *C. glomeratum* was also named as *P. conferta*. Collections on *C. fontanum* ssp. *vulgare* from a pasture near Penbryn and from the Ynys-las dunes in Cards had the sporangia $13-28 \times 13-24 \mu m$, globose to ellipsoid, many of them much smaller than the usually given lower limit of 18 or $22 \mu m$ for *P. conferta*, but many of them too large to be *P. paula*. Gustavsson (1987, 1991) is alone in giving the upper limit of the latter as $26.9 \times 20.7 \mu m$. Oospores are rarely found (see image on previous page). Recorded throughout Britain and Ireland. All year.

Peronospora conglomerata Fuckel

Confined to *Geranium* Crane's-bills and so far recorded in Wales mostly from Cards, whence there are a few records on *G. dissectum* Cut-leaved Crane's-bill, *G. lucidum* Shining Crane's-bill, *G. molle* Dove's-foot Crane's-bill and *G. robertianum* Herb Robert. Elsewhere it is reported from 13 sites in Carms and one in Caerns on *G. dissectum*, on *G. molle* from Aber in Caerns and Valley on Angl and on *G. lucidum* from near Llanrug, Caerns. Colonies on the leaf undersurface are greyish-white, the leaf becoming conspicuously yellowish above on *G. molle* whose infected leaves can sometimes be smaller. In the other species they are usually on older brownish and slightly decaying leaves and are thus less easily noticed. There are scattered records throughout Britain and Ireland, chiefly on *G. molle*. All year.



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Sporangium and sporangiophore of Peronospora conglomerata on Geranium molle



© DA Evans Peronospora conglomerata on Geranium molle

© DA Evans

Peronospora crispula Fuckel

Confined to *Reseda* Mignonettes and recorded in Wales on *R. luteola* Weld by the Ynys-las boatbuilding yard in Cards and on a field verge at Henfaes, Aber, Caerns. Colonies are greyish-white and prominent and cause large, elongated yellow-orange patches above. Recorded elsewhere in Britain only from Warwickshire and Surrey. Apr-Aug.

Peronospora crispula on Reseda luteola



Both images © DA Evans



[Peronospora cyparissiae de Bary

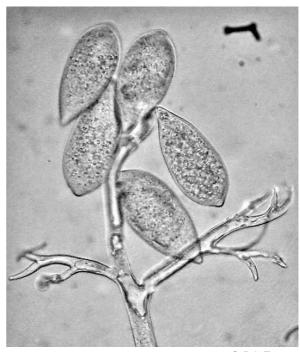
Confined to *Euphorbia* Spurges and in Britain recorded only on *E. cyparissias* Cypress Spurge in southern England and as close as Gloucestershire, but not yet recorded from Wales; the other species on *Euphorbia* in Britain is *P. euphorbiae* Fuckel, recorded on *E. amygdaloides* Wood Spurge, *E. paralias* Sea Spurge and *E. peplus* Petty Spurge with a similar distribution; a record of *P. valesiacae* Gäum. on *E. paralias* from Cornwall perhaps refers to this species.]

Peronospora destructor (Berk.) Casp. ex Berk.

Confined to *Allium* Onions, with old records for most of the Welsh vice-counties on *A. cepa* Onion, and one for Denbs on *A. ursinum* Ramsons, but surprisingly only one in the last 50 years (on cultivated Onions at Llangybi, Caerns). Colonies are pale greyish-violet on the leaves and stems, and the infection is systemic, dwarfing, distorting and ultimately often killing the plants; it causes severe losses in Onion crops. Commonly recorded throughout Britain and Ireland.

Sporangiophore and sporangia of Peronospora destructor (right)

Peronospora destructor on cultivated onion (below)



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Peronospora digitalidis Gäum.

Confined to *Digitalis* Foxgloves and recorded in Wales on *D. purpurea* Foxglove only from Caerns, Flints and Angl. Colonies are pale greyish or brownish-violet, causing brownish patches above and especially infecting young plants. There are scattered records from England and Scotland. May-Sept.

Peronospora dipsaci Tul. ex de Bary



Peronospora dipsaci on Dipsacus fullonum (above and right)

Confined to *Dipsacus* Teasels and with records only from Merthyr Tydfil, Glam in 2018, Llanelwedd, Rads in 2019 and from Banc y Lords, Carms in 1998, all on *D. fullonum* Wild Teasel. Colonies are dense and pale brownish-violet, chiefly on the younger rosette leaves which become pale, erect and distorted. (See image right of a year 1 rosette. The image above shows an infected plant to the left with erect leaves and uninfected plant with appressed leaves to the right). A repeat visit to Banc y Lords failed to relocate either Teasel or mildew in 2019. There are scattered records from England, mostly in the south. June-Oct.



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Peronospora effusa (Grev.) Rabenh.

Confined to *Spinacia* Spinaches (Choi *et al.* 2007), and recorded from Wales only once, by Vize in 1873 at Forden in Monts on *S. oleracea* Spinach. Yellowish, soon blackening patches appear on the leaves, with dense greyish, then violet colonies beneath, and the leaves soon wilt and die. Resistant races of Spinach are usually met by resistant races of the mildew, causing us significant problems in gardens and commercial crops. It is presumably much commoner than this one record indicates. Recorded throughout Britain and Ireland. June -July.

Peronospora ervi A. Gustavsson (P. viciae s.l.)

Probably widespread but easily overlooked and only noted on *Ervilia hirsuta* Hairy Tare in Wales. Some plants can, however, be quite severely affected by this pathogen, becoming stunted and with a greyish caste and can then be easily picked out amongst unaffected plants. Most records are from road verges but it has also been noted in un-mown grassland such as in country parks and churchyards and on sand dunes. There are recent records from Glam (1 site), Brecs (1 site), Rads (7 sites), Pembs (2 sites) Cards (1 site), Caerns (1 site) and Angl (1 site). A very similar looking downy mildew, possibly even this species, occurs outside Wales on *Ervum tetraspermum* Smooth Tare with one record close to the Welsh border to the west of Hereford (but see García-Blásquez 2008); it may occur in Wales. May-Aug.

Peronospora ervi on Ervilia hirsuta (right and below)



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Peronospora erythraeae J.G. Kühn ex Gäum.

Confined to Centaurium Centauries and recorded twice on C. erythraea Common Centaury in 2012 from coastal sites in Cards, on a bare patch on a steep grassy slope by the mouth of the Afon Soden, and by a sandy track alongside the Yacht Club at Penyrergyd. It was also reported inland on disused coal workings from near Tumble, Carms in 1998 and from a footpath edge beside Bettws Dingle, Bronydd, Rads in 2019. Colonies are greyish-white, and can be found throughout the plant. Recorded elsewhere in Britain only five times, in England, all on this host. May-Aug.



Peronospora erythraeae on Centaurium erythraea

© DA Evans

[P. euphorbiae Fuckel

See *P. cyparissiae* above].

[Peronospora fabae Jacz. & Sergeeva

Confined to, and the only downy mildew on, Vicia faba Broad Bean, and widely recorded in England (mostly as *P. viciae*), but not yet in Wales.]

Peronospora ficariae Tul. ex de Bary

Confined to Ficaria Celandines and one of the most conspicuous and frequently recorded downy mildews from most vice-counties in Wales. Where subspecies are specified, almost all records are on F. verna ssp. fertilis, Lesser celandine with only a few records on ssp. verna from Brecs, Rads, Cards, Monts and Mer. The colonies are visible from late January to early June, usually covering most of the lower surface of the leaves. Even before the sporangiophores (see image below right) emerge from the stomata, infected leaves can usually be reliably recognized as they tend to be upstanding on erect petioles, with the lamina edges curled down and usually slightly yellowish (see image below left). Infected

leaves also prematurely senesce. Oospores are usually present. It has been very commonly recorded throughout Britain and Ireland. Jan-June.



Peronospora ficariae on Ficaria verna ssp. fertilis

Peronospora ficariae sporangiophore

Peronospora flava Gäum.

Confined to Linaria Toadflaxes and recorded once on L. vulgaris Common Toadflax on a roadside hedgebank near Pennant in 2011, and once on L. purpurea Purple Toadflax in the walled garden at Llanerchaeron in 2019, both in Cards. The colonies were brownish and the leaves were yellowish, inrolled and curved. There is also a record on *L. vulgaris* from Haverfordwest, Pembs in 1993. It was formerly recorded under the name P. linariae, a taxon now considered to be confined to *L. repens* Pale Toadflax, Chaenorhinum minus Small Toadflax, L. arvensis Field Toadflax and Cymbalaria muralis Ivy-leaved Toadflax and which has much smaller sporangia 20-30µm (the Cards material of *P. flava* had sporangia 30-40µmsee image right). There is one other British record of P. flava, from Norfolk on Linaria vulgaris in 1944. March-Aug.



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Peronospora fulva Syd. (P. viciae s.l.)

Confined to *Lathyrus* Peas, there is one record each on *L. nissolia* Grass Vetchling from Mons and Glam, and very few records on this host and on *L. pratensis* Meadow Vetchling

from England and Scotland. The former plant is scarce across much of Wales and difficult to spot before or after its short flowering season. The downy mildew, however, turns the plant quite conspicuously yellow as the image below taken in Herefordshire illustrates.



© RG Woods

Peronospora fulva on Lathyrus nissolia

Peronospora galii Fuckel

Confined to *Galium* Bedstraws and so far recorded in Wales on *G. palustre* Common Marshbedstraw with records from Cards in a lawn at Ynys-hir in 2011, in Caerns by a skate park at Cwm y Glo and in Angl at Cors Erddreiniog; on *G. saxatile* Heath Bedstraw in an oakwood by the upper Tywi in 2014, and on *G. verum* var. *maritimum* Lady's Bedstraw on the Ynys-

las dunes in 2015 and on the sandy landward slope at the south end of Tan-y-bwlch beach in 2011, all in Cards. Colonies are greyish, with slightly pale or yellowish spots above, and infected shoots are often slightly etiolated and pale or yellowish. There are only a dozen or so other records scattered throughout Britain on these hosts and on G. album Hedge Bedstraw and *G. boreale* Northern Bedstraw. Apr-Sept.

Peronospora gei Syd.

Confined to Geum Avens, and recorded from Wales only at Loggerheads in Denbs on G. urbanum Wood Avens in 1976. Colonies tend to be small and greyish, with yellowish, then brownish patches above. There are scattered records throughout Britain.

Peronospora grisea (Unger) Unger

Confined to Veronica Speedwells. A common and conspicuous species on V. serpyllifolia Thyme-leaved Speedwell and V. beccabunga Brooklime and recorded on them in most of the Welsh vicecounties. Infected shoots, even before the sporangiophores emerge, can be recognized throughout the year, the shoots and leaves becoming pale vellowish and erect and flowering is usually, but by no means always, inhibited. The colonies are greyish, and usually cover the whole of the lower leaf surface (see image right of a sporangiophore). Very commonly recorded throughout Britain and Ireland on these hosts. There are two Welsh records on *V. montana* Wood Speedwell, one from from Mons and one from Brynea, Carms, though none from elsewhere in Britain.



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Peronospora grisea sporangiophores on a Veronica (Pseudoveronica) (=Hebe) sp. leaf



© DA Evans Peronospora grisea on Veronica beccabunga

© DA Evans



Peronospora grisea on Veronica serpyllifolia

© AO Chater

This mildew has also been recorded in Wales on what were formerly known as *Hebe* spp. (see image p53), now considered to be in subgenus *Pseudoveronica* of *Veronica*, in gardens at Portmeirion, Mer, Treborth, Caerns and at Benllech and Rhoscolyn on Angl. There are many records on this subgenus from elsewhere in England and Scotland. Jan-Oct.

Peronospora hariotii Gäum.

Confined to *Buddleja* Butterfly-bushes and recorded on *B. davidii* Butterfly Bush from Fishguard, Pembs in 2019, from Harlech, Mer in 2006, from Bangor in 2001 and 2014, Y Felinheli in 2004, 2011 and 2019 and Caernarfon in 2007, all in Caerns and from Llangefni, Angl in 2019. There are scattered records on this and *B. globosa* Orange-ball-tree in England. Colonies are greyish-violet, with yellowish patches above that become brownish. Apr-Dec.

Peronospora hariotii on young leaf of Buddleja davidii (right)



© DA Evans



© DA Evans Peronospora hariotii on Buddleja davidii leaves

© DA Evans

[Peronospora hiemalis Gäum.

Occurs only on *Ranunculus* Buttercups. Records from Cards on *R. acris* Meadow Buttercup, supposed to host only this species of *Peronospora*, all have the sporangia 20-27µm wide, so they would seem to be of *P. ranunculi* rather than *P. hiemalis* which has them only 17-18µm wide. Records on *R. acris* from elsewhere in Britain and Ireland require investigation, and there are no other records from Wales.]

Peronospora honckenyae (Syd. & P. Syd.) Syd.

Confined to *Honckenya peploides* Sea Sandwort and recorded at Burry Port in Carms in 1998, and pre-1879 in the same vice-county but with no location. There are scattered records in England and Scotland. Infected leaves are yellowish and distorted. May.

Peronospora jacksonii C.G. Shaw

Confined to Phrymaceae Monkeyflower family and described from North America. Once recorded in Wales, from Garn Lakes in Mons in 2005 on *Erythranthe* sp. Monkeyflower. The greyish colonies cause brownish patches above. There are three scattered records from England. Aug.



© DA Evans Peronospora jacksonii on Erythranthe sp.

Peronospora lamii A. Braun

Confined to *Lamium* Dead Nettles and *Lamiastrum* Yellow Archangel, and recorded in Wales only from Monts, in 1872 by Vize on *L. maculatum* Spotted Dead-nettle in his garden at



Peronospora lamii on Lamium maculatum



© RG Woods Peronospora lamii forming khaki patches on a leaf of Lamium purpureum also supporting white colonies of the fungus Ramularia lamii

Forden, and more recently in 2007 on this host at Four Crosses, Angl. Vize's record (as *L. rubrum*) was erroneously equated with *L. purpureum* in the FRDBI and in Preece (2002). On *L. purpureum* Red Dead-nettle there is but a single Welsh record from beside a flower bed in a car park in Builth Wells, Brecs. This mildew is widely recorded in England and Scotland, mostly on *L. purpureum*. March-June.

Peronospora linariae Fuckel

Confined to *Linaria repens* Pale Toadflax, *L. arvensis* Field Toadflax, *Chaenorrhinum minus* Small Toadflax, and *Cymbalaria* Toadflaxes. From Wales there is only a 1950 record on *Cymbalaria muralis* Ivy-leaved Toadflax from Betws-y-coed in Caerns. Elsewhere there are scattered records on this host throughout Ireland and one record from Devon. On *Chaenorrhinum minus* there is a single record from Suffolk. Colonies are greyish-white becoming brownish-violet and the leaves turn yellowish. See under *P. flava* above for confusion with this species, and all material requires careful checking or revision. Aug-Sept.

Peronospora lotorum Syd. (P. trifoliorum s.l.)

Confined to *Lotus*, Bird's-foot-trefoils, and recorded in Wales on *Lotus pedunculatus* Greater Bird's-foot-trefoil from Mons, Rads, Carms, Pembs, Cards, Monts and Angl but on *L. corniculatus* Common Bird's-foot-trefoil only from a road verge at Felinheli, Caerns. The colonies are greyish on the lower leaf surface causing pale or purple-coloured spots above, but are easily overlooked. May-Oct.



Peronospora lotorum on leaves of Lotus pedunculatus with discoloured upper leaf surface above left and lower surface above right with sporangiophores



Peronospora lotorum on Lotus corniculatus yellowing the upper leaf surface above left and with sporangiophores on the lower leaf surfaces above right

Peronospora mayorii Gäum. (P. viciae s.l.)

Confined to *Vicia cracca* Tufted Vetch. In Wales it is known only from a single road verge near Felinheli, Caerns where it was found in 2019. Infected leaves turn yellowish, whilst whitish sporangiophores occur scattered over the leaves. There are half a dozen records from England and Scotland. Sept.



Peronospora mayorii on Vicia cracca

Peronospora meconopsidis Mayor

Confined to *Papaver* Poppies and *Meconopsis* Blue-poppies. It has been recorded from most vice-counties in Wales and is widely reported in Britain and Ireland on garden and naturalized *Papaver cambricum* Welsh Poppy, where the colonies are greyish-white with rather sparse sporangiophores, causing pale yellowish patches above. Most of these



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Peronospora meconopsidis on Papaver cambricum (see also picture overleaf)

collections had sporangia >20µm, as given for this species by Voglmayr *et al.* (2014), but one collection from near Ponterwyd in Cards had them 17-20µm. It has also been found on *P. somniferum* Opium Poppy once in Caerns, in gardens at Llysdinam in Brecs and Knighton in Rads and at Ynys-hir in Cards; the sporangia in the latter site averaged >23µm, and the infection was clearly local, causing vein-delimited angular patches on the leaves and no distortion. This indicates that it is this species rather than *P. somniferi*, in which the infection



© AO Chater Peronospora meconopsidis on Papaver somniferum

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is often systemic, causing leaves or the whole plant to become pale and distorted, and the sporangia average 21.1µm, or even P. arborescens, which has the sporangia <20µm. Papaver somniferum is one of the very few host species to host two species of Peronospora, P. meconopsidis and P. somniferi (Voglmayr et al. 2014). There is also a 1939 record on Meconopsis betonicifolia Himalayan Blue-poppy from Monts. The distribution elsewhere in Britain is uncertain. Efforts should be made to establish whether this mildew occurs on truly wild populations of Welsh Poppy in Wales, as these are genetically distinct from most of the cultivated and naturalized populations. March-Oct.

Peronospora mecanopsidis yellowing a leaf of Papaver cambricum



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Peronospora melandryi Gäum.

Confined to *Silene* Sect. *Melandrium*, and recorded in Wales only on the leaves of *S. dioica* Red Campion on a lane verge near Bodedern, Angl in 2011. Colonies are greyish, with yellowish patches above. The only other British records are from Norfolk and Northumberland in the 1930s. Oct.

Peronospora melandryi on Silene dioica

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Peronospora meliloti Syd.

Confined to *Melilotus* Melilots and recorded in Wales only in Carms, from Penclacwydd in 1997, from Pwll in 1998 and from

Machynys in 2000 and 2019, on *M. altissimus* Tall Melilot, and from Mynydd Mawr colliery, Cwm Mawr in 1998 on *M. officinalis* Ribbed Melilot. Colonies are greyish-violet. There are scattered records from England. May-Aug.

Peronospora mesembryanthemi Verwoerd

Confined to Aizoaceae Dewplant family. There is a 1966 record from Abergavenny, Mons on *Dorotheanthus bellidiformis* (as *Mesembryanthemum criniflorum*) Livingstone Daisy. There

are no other British records on the FRDBI although it is known to horticulturists as a disease of various other ornamental species. Infection causes pale violet-greyish colonies and the leaves become yellowish to purplish and shrivel. June.

Peronospora minor (Casp.) Gäum.

Confined to *Atriplex* Oraches and recorded from several Welsh vice-counties on *A. patula* Common Orache and *A. prostrata* Spear-leaved Orache. Colonies are greyish, with yellowish patches above or the whole leaves or shoots become yellowish, distorted and reduced in size. The leaves should be carefully examined to establish the presence of the mildew since similar deformation of the plant occurs following aphid attack. There are scattered records of this mildew throughout Britain, mostly as *Peronospora arborescens* or *P. farinosa*. May-Sept.



© DA Evans Peronospora minor on Atriplex prostrata



Peronospora minor on Atriplex patula

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Peronospora myosotidis de Bary

Confined to *Myosotis* Forget-me-nots and *Brunnera* Greater Forget-me-nots and recorded in Wales only in Cards at three sites and in Caerns at one site, all on naturalized *Myosotis sylvatica* Wood Forget-me-not. Colonies are greyish, causing yellowish spots above, though no distortion occurs. There are scattered records on several species of *Myosotis* in Britain and Ireland. March-May.



© DA Evans Peronospora myosotidis on Myosotis sylvatica

© DA Evans

Peronospora obovata Bonord.

Confined to *Spergula arvensis* Corn Spurrey and recorded from half a dozen arable fields in Cards and from Henfaes, Aber, Caerns. Infected plants are quite conspicuous, the greyish colonies causing the infected stems and leaves to turn pale, yellowish and sometimes slightly distorted or etiolated. There are scattered records throughout Britain and Ireland. March-Sept.

Peronospora obovata on Spergula arvensis



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Peronospora oerteliana J.G. Kühn

Confined to *Primula* Primroses and Cowslips with recent records on *P. vulgaris* Primrose from Mons, Brecs, Carms and Flints. Vize recorded it in the 1870s from Monts and there is an 1866 record from Mer, and a solitary old record on *P. veris* Cowslip from Denbs. Colonies are pale greyish-violet, with yellowish patches above and with no distortion to the leaves. There are scattered records on these hosts from England and Scotland. May-July.



Peronospora oerteliana creating yellow patches on a leaf of *Primula vulgaris*

Peronospora ononidis G.W. Wilson (P. trifoliorum s.l.)

Confined to *Ononis* Restharrows and recorded only once in Wales, on *O. repens* Common Restharrow in 2014 on the Ynys-las dunes in Cards. Colonies are pale greyish-violet, with yellowish patches above and no distortion. The only other British record seems to be from Yorkshire pre-1905. May.

Peronospora ornithopi Gäum.



Peronospora ornithopi on Ornithopus perpusillus

Confined to *Ornithopus* Bird's-foots and recorded in Britain so far only on *O. perpusillus* Bird's-foot on Twt Hill, Caernarfon, Caerns in 2011. Infected leaflets are yellowish, with pale brownish-violet, rather thin colonies beneath. April.

Peronospora parva Gaüm.

Confined to *Stellaria* and recorded in Britain so far only on *S. alsine* at Hendy near Caernarfon in 2009 and at Parc Menai in 2019, both in Caerns, near Menai Bridge, Angl in 2014, and on *S. graminea* at Nant y Garth, Caerns in 2014. Colonies are greyish-white, infected leaves being pale or yellowish, often thickened and slightly distorted. The sporangia are smaller than those of *P. alsinearum*, which is also on *Stellaria* spp., averaging 19 × 16µm as against 27 × 22µm. Material on seedlings of *Stellaria pallida* in rabbit-grazed turf on the Ynys-las dunes, Cards, in 2019 had sporangia averaging 20.3 × 17.6µm, and abundant oospores in the leaves and stems, and were presumably this species even though Klenke & Scholler (2015) say that the mildew on *S. pallida* is *P. alsinearum*. Sept-Dec.



Peronospora parva on Stellaria alsine

Peronospora paula A. Gustavsson

Confined to *Cerastium* Mouse-ears and recorded in Wales from Mons, Carms and Cards on *C. fontanum* ssp. *vulgare* Common Mouse-ear. Colonies are greyish-white, causing infected parts to become pale, yellowish and sometimes slightly etiolated. It has the sporangia 13-20 × 12-18µm. Nine collections of *Peronospora* on this host from Cards have consistently small sporangia and are presumed to be this species, but the distinction between it and *P. conferta* is sometimes uncertain (see comments under *P. conferta*, and Gustavsson 1987). Oospores have rarely been found. Distinguishing another species, *P. fontana* A. Gustavsson from *P. paula* is difficult and the former, if distinct, may well be found to occur in Wales. Doubtless

widespread in Britain, with a recent record from as far north as the Outer Hebrides, though the only records in the FRDBI are from Yorkshire and Surrey. Jan-July.

Peronospora phlogina Dietel & Holw.

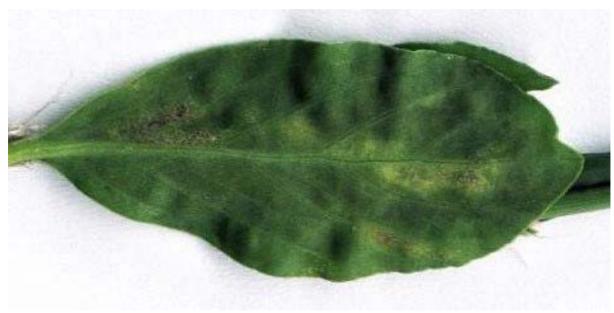
Confined to *Phlox* Phloxes and recorded on an annual species (perhaps *P. drummondii* Annual Phlox, the only normally cultivated annual) from Trawsgoed in Cards in 1969; the only other British record is on *Phlox* sp. from Yorkshire in 1989. Colonies are greyish, with yellowish patches on the leaves above, and are sometimes also on the stems. June-July.

Peronospora pisi DC.

Probably confined to *Lathyrus oleraceus* Garden Pea, but see García-Blázquez *et al.* (2008). There are old records from Mons, Glam and Monts, but it was and is doubtless much more widespread. It is a serious disease of pea crops and is widely recorded in England and Scotland. Colonies are whitish to pale violet, and infection can be systemic, killing the plants at seedling stage or later, or can only locally cause yellow patches on leaves or on the seed coats. Oospores are common in systemic infections (Spencer 1981). May.

Peronospora polygoni (Thün.) A. Fisch.

Confined to *Polygonum* s.l. Knotweeds and recorded in Wales only on *P. aviculare* Knotgrass near Aber, Caerns in 2008 and in Angl on the Aberffraw dunes in 2005. Colonies are greyish, with pale yellowish patches above. There are scattered records throughout Britain and Ireland on several of the host species. July-Aug.



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Peronospora polygoni on Polygonum aviculare

Peronospora potentillae-reptantis Gäum.

Confined to *Potentilla reptans* Creeping Cinquefoil and related species in the genus, and recorded on *P. reptans* from Glams, Caerns and Flints. Colonies are greyish-white, causing violet discoloration above. There are scattered records in England, on this host. June-Sept.

Peronospora potentillae-sterilis Gäum.

Confined to *Potentilla sterilis* Barren Strawberry and perhaps *P. recta* Sulphur Cinquefoil with records on the former from Rads, Carms and Cards. Infection is inconspicuous. The greyish colonies on the lower surface are often obscured by the hairiness of the leaves, though the mildew may also cause pale yellowish patches on the upper surface. Similar symptoms are, however often presented when the leaf is infected with the nearly ubiquitous rust fungus *Phragmidium fragariae* and so doubtless the downy mildew is easily overlooked. There are scattered records from England. May-Oct.



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Peronospora potentillae-sterilis on Potentilla sterilis (see also opposite)

[Peronospora radii de Bary

Confined to the Anthemideae in the Asteraceae Daisy family and recorded on several genera from England, but not yet from Wales; it differs from *Paraperonospora leptosperma* on similar hosts in occurring on the ligulate florets, as well as sometimes on the leaves.]



Peronospora potentillae-sterilis on Potentilla sterilis

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Peronospora ranunculi Gäum.

Confined to Ranunculus Buttercup species and recorded mostly on R. repens Creeping Buttercup but also on R. acris Meadow Buttercup, R. bulbosus ssp. bulbosus Bulbous Buttercup and R. flammula Lesser Spearwort, from most of the Welsh vicecounties. Colonies are greyish and usually dense and extensive, causing pale or yellowish spots or patches above, or often causing the whole leaf to be pale. The image right shows the whole plant of R. flammula discoloured and overleaf top right the sporangiophores on the leaves of R. flammula. On all eight specimens on R. acris collected in Cards the sporangia were all at least 20µm, and up to 27µm, wide, and thus within the range of P. ranunculi and too wide to be P. hiemalis, the species supposed to be on R. acris. This downy mildew is commonly recorded throughout Britain and Ireland, March-June.



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Peronospora ranunculi on Ranunculus flammula



Peronospora ranunculi on Ranunculus repens

© DA Evans © RG Woods Peronospora ranunculi on Ranunculus flammula

Peronospora romanica Săvul. & Rayss

Found only on Medicago Medicks, it is recorded on Medicago Iupulina Black Medick from six vice-counties in Wales and widely through Britain and Ireland. A vein-delimited yellowing of the upper leaflet surface betrays its presence, with a substantial greyish-violet colony on the lower surface. The sporangia are smaller (av. 20 × 17µm) and the oospores larger (av. >35µm) than those of P. aestivalis on M. sativa Lucerne (av. 27 × 20µm and <35µm). Apr-Sept.



Peronospora romanica on Medicago Iupulina

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Peronospora romanica on Medicago Iupulina

Peronospora rubi Rabenh. (P. sparsa s.l.)

Confined to *Rubus* Brambles and Raspberry and first recorded in Britain in 1973. It must still be quite rare (intensive recording has not revealed it in Carms or Cards), and it has been recorded on *Rubus fruticosus* agg. Bramble only in Glam, Brecs, Rads, Caerns and Angl, and on a *R. fruticosus* agg. × *R. idaeus* Bramble and Raspberry hybrid in Caerns and on *R. idaeus* in Flints. Colonies are whitish or pale greyish, with yellowish patches above. There are scattered records in England and Scotland on these hosts and on cultivated taxa. Sept-Oct.

Peronospora rumicis Corda

Confined to *Rumex* subgenus *Acetosa* Sorrels and found only rarely in Wales on *Rumex acetosa* ssp. *acetosa* Common Sorrel. Recurving of the leaves with a slight yellowing can indicate its presence. A search within the underside of the curled leaves then reveals the greyish colonies which can also occur sparingly on the upper leaf surface. Rarely, if the plants are heavily infected, the entire plant including the inflorescence takes on a greyish hue. In Wales it has been found three times in Rads, once in Pembs and twice in Cards. It has been very sparingly recorded in the rest of Britain and Ireland. May-June.



Peronospora rumicis on Rumex acetosa

Peronospora schachtii Fuckel (P. farinosa s.l.)

Confined to Beta Beets and recorded from Wales on Beta vulgaris ssp. maritima Sea Beet (see image right) from two beaches near Caernarfon, Caerns, from Penrhos, Angl, and from the "SW coast of Wales" in 1959. On ssp. vulgaris Sugar Beet it has been recorded in Cards (Ministry of Agriculture Bulletin 126: 29 (1942)). Colonies are greyish to dull violet in colour, and the leaves become yellowish and then redden, thicken and become distorted, inrolled and necrotic, usually starting in the



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Peronospora schachtii on Beta vulgaris ssp. maritima

centre of the rosette of young plants. Elsewhere in Britain it is widely recorded on both these subspecies and on various cultivars. It is a significant disease of Beet crops in many countries (see detailed account in Spencer 1981). Apr-May.

Peronospora senneniana Gonz. Frag. & Sacc.

Confined to Lathyrus Peas. A record on L. sylvestris Narrow-leaved Everlasting-pea from St Ishmaels in Carms in 2000, presumably of this species, along with one on *L. palustris* Marsh Pea from County Mayo in Ireland, may be the only ones from Britain and Ireland. Colonies are greyish-violet, with the leaflets pale above. May.

Peronospora sepium Gäum. (P. viciae s.l.)

Confined to Vicia sepium Bush Vetch and recorded from eight vice-counties in Wales. Leaves become yellow then pale greyish-violet with pale or yellowish patches above and with greyish colonies below (see image below right), but with no or only slight distortion, though heavily attacked shoots may be stunted. There are scattered records from England and Ireland. Apr-July.



Peronospora sepium on Vicia sepium

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Peronospora sherardii Fuckel

Confined to Sherardia arvensis Field Madder and found only once in Wales, at the edge of a Barley crop at Llwynysgaw, Cards in 2012. Colonies are greyish, causing the infected leaves to be conspicuously pale or yellowish. Oospores were not found. There are only six other British records, in England north to Yorkshire. Aug.

[Peronospora somniferi Voglmayr

Confined to *Papaver somniferum* Opium Poppy (Voglmayr, Montes-Borago & Landa, 2014) and differing from *Peronospora meconopsidis* on the same host in that the infection is systemic, is not limited to angular spots and often distorts the leaves. It has not yet been recorded in Wales.]

Peronospora sordida Berk. & Broome

Confined to *Scrophularia* Figworts and *Phygelius* Cape-figworts and recorded on *Scrophularia nodosa* Common Figwort from Carms, Cards, Caerns, Denbs, Flints and Angl, with old records from Rads, Monts and Mer, and on *S. auriculata* Water Figwort in Cards. Colonies are greyish, causing conspicuous yellowish patches above, which later become purplish-brown. There are scattered records throughout Britain and Ireland on *S. nodosa* and *S. auriculata*. Apr-Oct.



Peronospora sordida on Scrophularia nodosa

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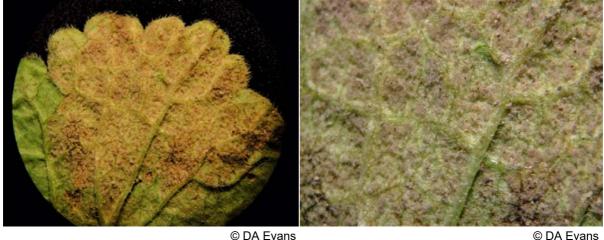
Peronospora sparsa Berk.

Confined to *Rosa* Roses and *Prunus laurocerasus* Cherry Laurel and first recorded in Britain in 1862. On the latter host it has been recorded from Glam (Preece 2002). On a cultivar of *Rosa* it has been recorded post 1985 from Caerns (Preece 2002). On *Rosa* greyish-white colonies on the lower surface of the leaves produce reddish, yellowish or blackish variegated patches above, and it also infects stems, calyces and petals and can cause whole shoots to die. On the *Prunus* it causes large, well-defined yellowish-brown unsightly patches above. It is recorded throughout England on *Rosa* cultivars, chiefly in greenhouses, with one record on *R. spinosissima* Burnet Rose and a few on *Prunus laurocerasus*. Sept.

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Peronospora stachydis Syd.

Confined to Stachys, and recorded in Britain only on S. arvensis Field Woundwort in 2011 in an arable field near Llanrwst, Denbs. Colonies are greyish or violet-tinged on the lower leaf surface with conspicuous yellowish patches becoming brown above. July.



Peronospora stachydis on Stachys arvensis

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Peronospora symphyti Gäum.

Confined to Symphytum Comfreys, and recorded in Wales only from Flints, on S. officinale Common Comfrey. Colonies are brownish and show blackish patches above. There are scattered records on several species of Comfrey from England and Ireland. Seasonality unknown in Wales.

Peronospora tabacina D.B. Adam



Peronospora tabacina on Nicotiana sp.

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Confined to Solanaceae, and recorded in Wales from Tenby in Pembs in 1997 on *Nicotiana* cvs. and in 2007 in Caerns on *N. sylvestris* cv. in a garden conservatory at Llandegai. In 2012 it was noted on *N. tabacina* in the garden at Plas Newydd, Angl, and in 2019 in the garden at Plas yn Rhiw, Rhiw, Caerns. First recorded in Britain in 1958, and since then occurring on various cultivars of *N. tabacum* and other species in this genus. Known as "blue mold" in America, the pale bluish colonies on the undersurface of leaves cause chlorotic patches on the upper leaf surface and shriveling of the leaves, and it can kill the host in a few weeks. It is a serious pest of Tobacco growing in many countries and is a notifiable disease in Britain. June-Sept.

Peronospora tomentosa Fuckel

Confined to *Cerastium* Mouse-ears. The sporangia on collections of downy mildews from Cards on *C. glomeratum* Sticky Mouse-ear, on which the only species in Britain and Europe is said to be *P. tomentosa*, have sporangia varying greatly in size. Most of the collections are entirely within the range given by Klenke & Scholler (2015), 13-22 × 12-17µm, but 24 have the sporangia variously larger and up to 25 × 18(-20) µm. Whether all of these latter are also *P. tomentosa*, or whether some are *P. conferta* or another species, and indeed whether the two species are really distinguishable, remains to be investigated. The Klenke & Scholler range is itself much larger than the 16-17 × 13-14µm given by the website (Obligat) Phytoparasitische Kleinpilze http://jule.pflanzenbestimmung.de/. Infection has the same effect as with *P. conferta* and *P. paula*. Oospores have not been found. There are also records from Mons, Brecs, Rads, Carms, Monts, Mer, Caerns and Angl and it appears to be a common species. There are scattered records elsewhere throughout Britain. All year.





© RG Woods Peronospora tomentosa on Cerastium glomeratum

© RG Woods

Peronospora trifolii-arvensis Syd.

Confined to *Trifolium* Clovers and recorded rarely on *T. dubium* Lesser Trefoil from Mons, Brecs, Rads, Carms and Flints, despite the abundance of the host. It was found on roadside verges in Brecs and Rads that all appeared to have been cut in late spring. Nearby unmown

host plants appeared to be un-infected. The one meadow site in Rads had experienced heavy late-spring grazing so in all of these sites the infected individuals of this annual clover may have had to regrow. Viewed from above a slight yellowing of a leaflet alone betrays the presence of this mildew so it may have been widely overlooked. In both Brecs sites and in one Rads site the host was also infected with the rust fungus *Uromyces minor*. There are very few records of the mildew on this species elsewhere in England and Scotland. Klenke & Scholler (2015) assign the mildew on *T. dubium* to *P. trifolii-arvensis*, but Garcíá-Blazquez *et al.* (2008) assign it, along with the other species in Section Chronosemium, to *P. trifolii-minoris* Gäum. May-July.



Peronospora trifolii-arvensis and the rust fungus Uromyces minor on Trifolium dubium

Peronospora trifolii-hybridi Gäum.

Confined to *Trifolium* Clovers. Using the taxonomy of Klenke & Scholler (2015) this species has been recorded on *T. pratense* Red Clover in a hay meadow at Llangwathen, Hay on Wye, Brecs and on waste ground at Llwynysgaw in Cards, and from scattered sites elsewhere in Britain and Ireland. There is also a 1959 record on *T. hybridum* Alsike Clover from Denbs, and several from the north and west of England and Scotland. García-Blázquez *et al.* (2008) agree that the species on *T. hybridum* is *T. trifolii-hybridi*, but they assign the mildew on *T. pratense* to *P. trifolii-pratensis* A. Gustavsson. The colonies are greyish causing inconspicuous pale to brownish spots above. May-June.



© RG Woods Peronospora trifolii-hybridi on Trifolium pratense

© RG Woods

Peronospora trifoliorum de Bary s.l.

Confined to Trifolium, and recorded on both T. medium Zig-Zag Clover and T. repens White Clover from Rads and Flints and from scattered localities throughout England and Scotland. It causes distinctive yellowing of the leaves in Zig-Zag Clover though sporulation seems to be delayed on the lower surface of the leaves for some time after the discoloration is apparent. The three Rads records were from road verges, that on White Clover being on a large-leaved cultivar. Despite the abundance of White Clover this mildew seems to be genuinely rare. Note that García-Blázquez et al. (2008) assign the mildew on T. medium to P. trifoliorum s.s., and that on T. repens to P. trifolii-repentis Syd. Apr-Sept.



© RG Woods Peronospora trifoliorum on Trifolium medium

Peronospora valerianae Trail

Confined to *Valeriana* Valerians and recorded in Wales on *V. officinalis* Common Valerian in damp woodland at Felinheli and on a river bank at Pentir, both in Caerns and at Llyn Alaw and Llyn Maelog on Angl. The pale greyish-violet colonies have yellowish patches above, and cause no distortion of the leaves. There are several records on this host from England and Scotland. April-Sept.



Peronospora valerianae on Valeriana officinalis

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Peronospora valerianellae Fuckel

Confined to *Valerianella* Cornsalads and recorded in Wales once on *V. carinata* Keel-fruited Cornsalad at Aberystwyth in 2001, and once on *V. locusta* Common Cornsalad at

Llanbadarn Fawr in 2003, both sites in Cards. The pale greyish-violet colonies cause paleness on the leaves above, but do not appreciably distort the plant and are inconspicuous. There are a very few records on both these hosts from England and Scotland. Apr-June.

Peronospora verbenae U. Braun, Jage, A.U. Richter & H.J. Zimmerman

Confined to Verbena, this mildew was first noted in Germany and in Wiltshire in 2007 and in 2009 was found in the Czech Republic (Choi et al. 2010). In Wales it was first recorded in 2019 on the leaves of a *V. officinalis* Vervain cultivar in a flower bed in the walled garden at Glynhir Mansion near Llandybie, Carms. It was subsequently found in the garden at Llanerchaeron, Cards and on wild plants in a farmyard at Llanedi in Carms. The older leaves developed conspicuous purple patches on the upper



© RG Woods Peronospora verbenae on Verbena officinalis



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Peronospora verbenae on Verbena officinalis

surface. The pale lilac-grey colonies were less conspicuous but fairly dense on the lower leaf surfaces (see image above). The plant in the Glynhir walled garden had been grown from seed and had presumably subsequently been infected. July-Aug.

Peronospora viciae (Berk.) Casp. s.s.

In the strict sense confined to *Vicia* Vetches and recorded in Wales only on *V. sativa* Common Vetch and its segregates, ssp. *nigra* and ssp. *segetalis*, from nine vice-counties, and on *V. lathyroides* Spring Vetch on the Ynys-las dunes in Cards in 2019, but it is probably ubiquitous. Colonies are rather sparse and greyish-white, but cause whole younger shoots to become conspicuously yellowish and somewhat stunted though otherwise not distorted; in some years it can be extremely common. Oospores are often found. Commonly recorded throughout England and Scotland on *V. sativa*. March-Dec.

Peronospora viciae s.l.

García-Blázquez *et al.* (2008) indicate uncertainty about the validity of some of the segregates recognized here (following Klenke & Scholler 2015) on *Vicia* s.l. and *Lathyrus*, and records on *Vicia orobus* Wood Bitter-vetch from Rads and *Lathyrus odoratus* Sweet Pea from Cards, Pembs and Mer mostly in the 1960s seem best placed here until further information is available. The presence of a downy mildew on *V. orobus*, a long-lived



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Peronospora viciae s.s. on Vicia sativa

perennial vetch, in a single agriculturally unimproved hay meadow in the Elan Valley, Rads had been recognized for some years by one of the authors but only of late has it become clear that there seem to be no other localised records on this host (see Preece 2002). Infected plants become stunted and yellowish (see upper image overleaf), though heavily infected shoots turn brown and die.

The meadow is grazed until late May by sheep and lambs and the first growths of *V. orobus* shoots are often grazed off. It is the later-produced stems that seem susceptible to this



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Peronospora viciae s.l. on Vicia orobus Wood Bitter-vetch



©RG Woods

Peronospora viciae s.l. on Vicia orobus Wood Bitter-vetch

parasite which reduces the vigour of plants but still allows some flowering to occur in some infected plants. Nearby ungrazed populations of the vetch show no sign of this mildew. As remarked in the introduction *V. orobus* is one of the few British plants with stomata confined to the upper leaf surfaces. Sporangiophores are more abundant on this upper surface (see image above) but some still occur on the lower leaf surfaces where groups of them are able to penetrate small necrotic areas of the lower epidermis to shed their spores. March-Dec.

Peronospora violacea Berk. ex Cooke

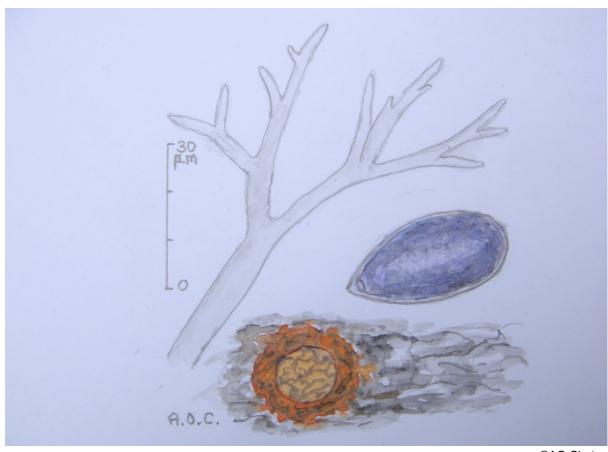
Confined to Dipsacaceae Teasel family, and recorded in Wales from fens, marshy pastures and road verges at 14 sites in Cards, two sites in Brecs and one each in Mons, Rads, Pembs and Mer, all on *Succisa pratensis* Devil's-bit Scabious. The colonies are, unusually for *Peronospora*, in the flowers, and infected inflorescences have all or many of their corollas brownish and dead-looking, with strongly violet-coloured sporangia on the outside and more abundant ones inside, as well as on the styles and filaments. Oospores are abundant within the corolla tissue, sometimes in the complete absence of sporangia in the corollas. There are scattered records on *Knautia* Field Scabiouses and *Scabiosa* Scabiouses from England and Scotland, but on *Succisa* only an old one from Scotland and recent ones from Cambridgeshire, England. Sept-Oct.

We are fortunate in having discovered a number of colonies of this little-reported mildew and provide additional illustrations on the rear cover. M. C. Cooke in his *Rust, Smut, Mildew & Mould. An Introduction to the Study of microscopic Fungi*, ed. 6 in 1898, could only provide a very brief description in Latin. The Rev. M.J. Berkeley, finder then of the only known British specimen had apparently "either lost or mislaid my specimens"! *Peronospora knautiae* Fuckel ex L. Schröt. has been recorded on *Knautia arvensis* Field Scabious in Cambridgeshire, and on *Scabiosa* in Europe, and differs in occurring on the leaves where it forms greyish or brownish-violet colonies with dark spots above.



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Peronospora violacea turning brown the above right inflorescence of Succisa pratensis



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Drawings (not to scale) of *Peronospora violacea* with to the top left a sporangiophore, at the lower centre an oospore and to the centre right a sporangium

Peronospora violae de Bay ex J. Schröt.



Peronospora violae on Viola arvensis (left) and sporangiophores (right)



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Peronospora violae on Viola arvensis

Confined to *Viola* Violets on both annual and perennial species, and recorded on *V. arvensis* Field Pansy from fallow and arable fields in two sites in Rads, one in Carms, five in Cards and one in Denbs and on *V. riviniana* Common Dog-violet from St Ishmaels in Carms in 2001 and on *Viola* sp. in Monts in the 1870's (Vize 1879). Colonies are greyish on the lower surface of leaves, causing large yellowish or brownish patches on the upper surface. There are scattered records throughout England, where it is a well-known parasite of cultivated *V. xwittrockiana* Garden Pansy. June-Aug.

Peronospora sp. on Aquilegia

In 2000 plants of *Semiaquilegia* False Columbines in South Korea were reported infected by a species of *Peronospora*, and in 2013 it was confirmed as infecting *Aquilegia* Columbine species in Britain (although symptoms of it had been seen for several years previously). Since then it has become widespread in Britain with a major impact in gardens and nurseries (Denton *et al.* 2015). Oospores are formed. So far it has not been named or formally described as a new species. It was found in Cardiff, and in the National Collection of *Aquilegia* at Killay, Swansea, Glamorganshire, in 2014, and has since so devastated the associated Touchwood Plants and Seeds that it has ceased trading. See http://www.touchwoodplants.co.uk/aquilegia-downy-mildew.htm for a full, well-illustrated and harrowing account of the impact of this mildew on the collection from which with consent and thanks we have drawn the images below. The mildew was found in the National Botanic

Garden of Wales, Carms in 2015 and in May 2019 in a garden 7km to the north of this latter site at Felingwm. In the same month *Aquilegia vulgaris* Columbine plants were found infected in a garden at Llanigon in the Wye Valley, Brecs. Chlorotic vein-delimited patches develop on the leaves, gradually spreading and becoming purplish, ultimately stunting growth, curling the leaflet margins, inhibiting flowering and leading to the death of the plant. In Britain *A. vulgaris* is the main host, but several other garden species including *A. alpina*, *A. flabellata*, *A. viridiflora* and several cultivars and hybrids have been infected. May.





© Touchwood Plants Peronospora sp. on Aquilegia vulgaris

© Touchwood Plants

Peronospora sp. on Suaeda

A Peronospora has been recorded from several countries in Western Europe on Suaeda maritima Annual Sea-blight and was found new to Britain beside the Inland Sea, near Valley, Angl on this species in 2008. The rather sparse, whitish colonies cause the leaves to be slightly pale but scarcely enlarged or distorted. Its identity remains uncertain; the species on the related genus in the Amaranthaceae Goosefoot family in Europe, Salsola Saltworts, is P. vistulensis Wrób. Aug.



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Peronospora sp. on Suaeda maritima

Plasmopara J. Schröt.

Parasitic chiefly on members of the Apiaceae Umbellifers, but also on several other groups in Wales. Haustoria in the host tissue are vesicular and entire. Colonies are predominantly white and dense. Sporangiophores are monopodially branched, the primary branches at 45° or more (see image below right); apices of sporangiophores are blunt, closed by a new wall after the sporangia have detached (see image below left). The sporangia produce zoospores. Fourteen taxa have been reported from Wales.



© AO Chater Plasmopara sp. sporangiophores

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Plasmopara angelicae (Casp.) Trotter (P. crustosa s.l.)

Confined to Angelica Angelicas and recorded on A. sylvestris Wild Angelica from 11 vicecounties in Wales; it is often very common. Colonies are whitish, not very dense, and cause yellowish-brown patches above. Widely recorded throughout England and Scotland. May-Nov.



Plasmopara angelicae on Angelica sylvestris

© TE Greenaway

Plasmopara chaerophylli (Casp.) Trotter (P. crustosa s.l.)

Confined to *Anthriscus* and *Chaerophyllum* Chervils and in Wales recorded 35 times on *Anthriscus sylvestris* var. *sylvestris* Cow Parsley from seven vice-counties, including an old record from Flints. It is inconspicuous, the whitish colonies on the lower surface of the leaf with pale geen patches above, turning bronze, and causing no distortion to the leaves. It is doubtless more widespread than the records currently suggest. It has been widely recorded in England and Scotland and is known in England also from *Chaerophyllum temulentum* Rough Chervil. Apr-Oct.



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Plasmopara chaerophylli on Anthriscis sylvestris

[Plasmopara crustosa (Fr.) Jørst. s.l. and P. umbelliferarum (Casp.) J. Schröt.

Plasmopara species on Apiaceae were usually referred to *P. crustosa*, *P. nivea* or *P. umbelliferarum* in older literature. *P. crustosa* (Fr.) Jørst. s.s., now confined to *Heracleum* Hogweeds, has been recorded from a few sites in Britain and Ireland, but not in Wales, and *P. umbelliferarum* (Casp.) J. Schröt. s.s. does not occur in Britain. See Constantinescu (1992).]



Plasmopara densa (Rabenh.) J. Schröt. (P. crustosa s.l.)

Confined to Orobanchaceae Broomrape family, and recorded in Wales on Odontites vernus Red Bartsia from seven vice-counties, and with an 1870s record by Vize from Forden in Monts, and on Rhinanthus minor Yellowrattle from nine vice-counties and again with an additional Vize record from Forden. On both hosts it is often common and is probably present throughout Wales. Colonies form a dense white felt on the lower surface of the leaves, with little or no effect on the shape of the leaf above, though the upper surface often becomes conspicuously yellow. On O. vernus the upper surface may become purple streaked. It has been commonly recorded throughout Britain and Ireland on the above hosts and from Scotland on both *Pedicularis palustris* Marsh Lousewort and R. angustifolius Greater Yellowrattle. Apr-Sept.

Plasmopara densa on Rhinanthus minor



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Plasmopara epilobii (G. H. Otth) Sacc. & P. Syd.

Confined to *Epilobium* Willowherbs, there is a 1988 record from Coed Gorswen, Caerns on *Epilobium* sp. and a couple of records from England on *E. montanum* Broad-leaved Willowherb and *E. parviflorum* Hoary Willowherb. The colonies are whitish on the leaf lower surface and yellowish or brownish above. Sept.

Plasmopara euphrasiae Voglmayr & Constant.

Confined to *Euphrasia* Eyebrights, it has been recorded 17 times from five vice-counties on various *Euphrasia* taxa, but as it develops late in the season and the mildew sometimes causes the plant to be deformed or prevented from flowering, it is not always possible to identify the host. There are records from Cards on *E. confusa* × *nemorosa*, *E. officinalis* ssp. *anglica* English Eyebright, *E. confusa* × *tetraquetra*, *E. nemorosa* Common Eyebright, from

Carms on E. confusa x nemorosa, E. officinalis ssp. pratensis Rostkov's Eyebright and E. arctica ssp. borealis Arctic Eyebright, and from Mons, Mer and Caerns on E. officinalis agg. Most records are from the verges of roads or forestry tracks in the uplands, up to 410m altitude. Colonies are whitish and fairly dense, on leaves, bracts and often calyces. It was formerly included in Plasmopara densa but described as a new species confined to Euphrasia on morphological and molecular grounds by Voglmayr &



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Plasmopara euphrasiae on Euphrasia officinalis

Constantinescu (2008). It has been sparingly recorded in Britain, mostly in the north. July-Sept.

Plasmopara nivea (Unger) J. Schröt. s.l.

Occurring in the broad sense on various genera in the Apiaceae Carrot family, this taxon is

awaiting detailed taxonomic revision. For further information see Constantinescu et al. (2005). Recorded in Wales on Conopodium majus Pignut from ten vice-counties; the colonies are inconspicuous, sparse and whitish, often on only a few leaf segments which are paler and ultimately become brown and necrotic, but otherwise undistorted. On Oenanthe crocata Hemlock Water-dropwort it has been recorded from six vice-counties, the colonies being more conspicuous. On Smyrnium olusatrum Alexanders it has been recorded from Caerns and Angl. A record on Ligusticum scoticum Scots Lovage in 2015 in a garden at Eglwys-fach in Cards probably also belongs here. March-Oct.



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Plasmopara nivea s.l. on leaf of Conopodium majus



Plasmopara nivea s.l. on Conopodium majus

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Plasmopara nivea s.l. on Smyrnium olusatrum

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Plasmopara nivea s.l. on Oenanthe crocata

Plasmopara nivea J. Schröt. s.s. (P. crustosa s.l.)

In the strict sense *P. nivea* is confined to *Aegopodium* Ground Elders and is recorded on *A. podagraria* Ground Elder from 12 vice-counties in Wales, being often common where it occurs. Colonies on the lower surface of the leaf are bright white, dense and well-defined, with pale or slightly yellowish patches above (see image opposite). It has been widely recorded throughout Britain and Ireland. Feb-Sept.

Plasmopara obducens (J. Schröt.) J. Schröt.

This mildew, confined to *Impatiens* Balsams, was first found in Britain in 2003, infecting *Impatiens walleriana* Busy Lizzie. It was effectively controlled for several years by the systemic fungicide Metalaxyl, but became more frequent from about 2007 and in 2011 the mildew was found to have developed resistance to the fungicide. It then spread rapidly and devastated Busy Lizzies throughout Britain, the infected leaves rotting and the plants rapidly dying. *Impatiens*



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Plasmopara obducens on Impatiens walleriana



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Plasmopara nivea s.s. on Aegopodium podagraria

hawkeri New Guinea Busy Lizzie is resistant and various cultivars of it have now replaced *I. walleriana* in the very lucrative horticultural bedding plant trade. It is not clear how serious the disease was in Wales, though it was presumably ubiquitous. It was seen in Mons in 2011 (Evans 2011) and in a Butterfly House in Cwm Rheidol in Cards in the same year. This, and a 2003 record of *Plasmopara* sp. on *Impatiens* sp. from England in 2003 are surprisingly the only records in the FRDBI. Unfortunately, it seems not to infect *I. glandulifera* Himalayan Balsam, a very troublesome alien in Britain. Aug.

Plasmopara pastinacae Săvul. & O. Săvul. (P. nivea s.l., P. crustosa s.l.)

Confined to *Pastinaca* Parsnips and recorded on *P. sativa* Parsnip only from Glam in 1931, although doubtless more widespread. Colonies cause whitish patches on the younger lower leaf surface and yellowish and brown vein-delimited patches above. It is widely recorded from England, mostly in the south. Seasonality unknown in Wales.

Plasmopara pimpinellae Săvul. & A. Săvul. (P. crustosa s.l.)

Occuring only on *Pimpinella* Burnet-saxifrages, it has been recorded twice in Wales on *P. saxifraga* ssp. *saxifraga* var. *saxifraga* Burnet-saxifrage. The mildew was found in small quantity in a large population of its host in a species-rich agriculturally unimproved field near Beulah, Brecs and on a roadside above Borth in Cards, both in early August. The infected



Plasmopara pimpinellae on Pimpinella saxifraga ssp. saxifraga

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leaves become distinctly copper-coloured and sometimes swollen and the whitish colonies are rather sparse in occurence. Elsewhere in Britain there is only an 1889 record on P. saxifraga from North Aberdeen, a 2007 record from Derbyshire and a 2002 record on P. major Greater Burnet-saxifrage from Yorkshire. Aug.

Plasmopara pusilla (de Bary) J. Schröt. s.s.

Confined to Geranium Geraniums, the sole recent record from Wales was on G. pratense Meadow Cranesbill in a flower bed at Henllys Hall, Llangoed, Angl in 2019. Infected plants were conspicuous with the mildew creating whitish colonies on the lower leaf surfaces and yellowish patches on the leaves above. There is one earlier record on this host from beside the River Teme near the bridge in Knighton Rads in 1969. Its rarity in Wales is difficult to explain since it is widespread on this host in England and Scotland.



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Plasmopara pusilla on Geranium pratense

A 1928 record from G. sylvaticum Wood Crane's-bill from Llanfrynach in Brecs (the host no longer being known from this area) and records on G. pyrenaicum Hedgerow Crane's-bill from Flints and in a hedgerow by a car park in Newborough Forest, Angl require investigation. They could be P. praetermissa Voglmayr, Fatehi & Constant., or P. geraniisylvatici Săvul. & O. Săvul. which is what the mildew on G. sylvaticum is in Germany (M. Thines pers. comm.) and are meanwhile best considered to be of *P. pusilla* s.l. July-Oct.

Plasmopara saniculae Săvul. & O. Săvul.

Confined to Sanicula europaea Sanicle and recorded in Wales only by Vize from Forden in Monts in 1874. Colonies are whitish, with brownish, vein-delimited patches above. There are scattered records from England and Scotland. May.

[Plasmopara umbelliferarum (Casp.) J. Schröt.

See Plasmopara crustosa.]

Plasmopara viticola (Berk. & M. A. Certis) Berl. & De Toni

A serious parasite of commercial vinyards, it is confined to Vitis Grape-vines. In Wales it has been recorded on V. vinifera Grape-vine from Llanfihangel Ystern Llewern in Mons in 2006 and on V. vinifera 'Purpurea' from Machynlleth in Monts in 2019. The white colonies cause pale patches on the leaves that become reddish-brown; leaves, young shoots and fruits are often heavily infected and on young fruits especially the white covering looks very similar to the powdery mildew Erysiphe necator. There are scattered records in the south of England on this host and V. coignetiae Crimson-glory Vine. Sept.





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Plasmopara viticola on V. vinifera "Purpurea" Sporangiophore of Plasmopora viticola

Plasmoverna Constant., Voglmayr, Fatehi & Thines

Differs from *Plasmopara* in that the blunt apices of the sporangiophores remain open after the sporangia have detached (see image right). Confined to Ranunculacae (Constantinescu *et al.* 2005).

Plasmoverna pygmaea (Unger) Constant., Voglmayr, Fatehi & Thines





© AO Chater Plasmoverna sporangiophore (left) and Plasmoverna pygmaea on Anemone nemorosa (right)

This species occurs on several genera of the Ranunculaceae Buttercup family, and is common and conspicuous on *Anemone nemorosa* Wood Anemone with over 50 records from 12 vice-counties in Wales. Colonies on the lower surface of the leaves are white, defined by the veins, and cause pale or yellowish patches above, becoming grey-brown with



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Plasmoverna pygmaea on Anemone nemorosa

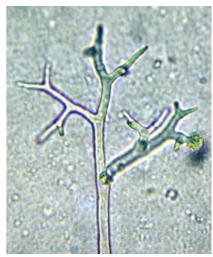
age and prematurely killing the leaves. It is listed by Preece (2002) as one of the most commonly recorded species throughout Britain and Ireland. There are records from Pembs in 1958 and Cards in 1960 on *A. coronaria* Poppy Anemone. Apr-June.

Pseudoperonospora Rostov.

Parasitic on several families, including Cannabaceae Hop family and Urticaceae Nettle family in Wales. Haustoria are hypha-like and branched. Colonies are brownish-grey. Sporangiophores are monopodially branched, the primary branches at 45° or more, and the apices of the sporangiophores are pointed (see image right). The sporangia produce zoospores.

Pseudoperonospora humuli (Miyabe & Takah.) G.W. Wilson (*P. cubensis* (Berk. & M. A. Curtis) Constant. s.l.)

Confined to *Humulus* Hops, and probably widespread in Wales on H. lupulus Hop where it is naturalized in hedgerows, the mildew becoming systemic. It is common in roadside hedges just to the west of Abergavenny, Mons, near Llanfihangel Talyllyn and at Ty Mawr Mill, Llysdinam, both in Brecs, near Painscastle, Heyop and Clyro in Rads and around Ffynnon Bedr Chapel near Drefach and in the National Botanic Garden of Wales, Carms. Despite extensive searches it has only been found twice in Cards, in scrub in Llanina churchyard and in a garden hedge at Ynys-las, although this host is frequent in hedges throughout the county. Heavy infections are unmistakable with the young shoots stunted and the leaves quickly turning yellow and then becoming patchily brown. Leaves and stems become covered in greyish-coloured colonies. There are scattered records in England north to Herefordshire. May-Aug.



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Pseudoperonospora humuli on Humulus lupulus



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Pseudoperonospora humuli on Humulus lupulus

Pseudoperonospora urticae (Lib.) E. S. Salmon & Ware

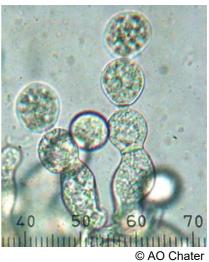
Confined to *Urtica* Nettles and found recently in only three vice-counties in Wales, on *Urtica dioica*, Common Nettle in Mons in 2008, in early December 2019 at Cwmbach in Glam and on a road verge south of Blaenannerch, Cards at the end of September in 2016. There are old records from Berriew in Monts by Vize in 1874, and a more recent record from Flints in 1978. The colonies on black spots on the lower surface of the leaves are greyish-brown, but small and inconspicuous, with no distortion of the leaves. At the Cards and Glam sites it was mixed with the much more conspicuous hyphomycete *Ramularia urticae*. It is probably overlooked. There are scattered records throughout Britain and Ireland. *Peronospora debaryi* occurs on *U. urens* Annual Nettle elsewhere in Britain, and as close as Shropshire, causing distortion and dwarfing of the leaves. Salmon & Ware (1929) describe the two species in great detail. May-Dec.

Albuginaceae

Haustoria are vesicular, globose and small. Sporangiophores are short, clavate, entire and dense, and develop in distinct sori under the cuticle of the host leaf so that the colonies have a shiny white crust; the hyphae are aseptate. The sporangia produce zoospores. There are two genera and nine taxa in Wales.

Albugo (Pers.) Roussel

Parasitic on various genera of the Brassicaceae Cabbage family and on *Spergula arvensis* Corn Spurrey and *Spergularia* Sea-spurreys in the Caryophylllaceae Pink family in Britain, forming pustules with shiny white crusts on the lower leaf surfaces and other parts of the plant. The infection can lead to a yellowing of leaves and stems and occasionally extreme distortion. Only one type of sporangium is formed, thin-walled and colourless. For a review of the taxonomy, including the separation of *Pustula* and *Albugo*, see Thines & Spring (2005) and Constantinescu & Thines (2006). Seven taxa are reported from Wales.



Sporangiophores and sporangia of *Albugo candida* s.l.

Albugo candida (Pers.) Roussel s.l.

Common (though so far under-recorded) on many Brassicaceae Cabbage family taxa. Five



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Albugo candida s.l. on Sisymbrium officinale

segregates of the mildew occur in Wales in addition to A. candida s.s., with more no doubt still to be described. It is infamous amongst gardeners for its ability to infect a wide range of cultivated Brassicas, distorting leaves and covering them with conspicuous white pustules. We have, however, been able to locate surprisingly few records. It is noted on the following varieties of Brassica oleracea: var. gemmipara Brussel Sprout, var. viridis Kale and var. botrytis Cauliflower/Broccoli from Cards and on this latter var. also from Caerns together with var. capitata Cabbage and with a pre-1970 record from Mons on var. medullosa Marrowstem Kale. The remaining records comprise those on 20 taxa in 15 genera: Cardamine flexuosa Wavy Bittercress, in ten vice-counties; Lunaria annua Honesty in seven; Sisymbrium officinale Hedge Mustard in five; Cochlearia officinalis Common Scurvygrass and Raphanus raphanistrum subsp. maritimus Sea Radish in four; Brassica rapa subsp. campestris Wild Turnip and Lobularia maritima Sweet Alison in three; and Barbarea verna American Winter-cress, Cakile maritima Sea Rocket, and Cochlearia danica Danish scurvygrass in two



Albugo candida s.l. on leaves of Lunaria annua



© DA Evans © DA Evans Albugo candida s.l. on Cakile maritima (above left) and Cochlearia officinalis (above right)



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Albugo candida s.l. on Cochlearia officinalis

being amongst the most frequently recorded hosts. There are further records from single vice-counties on *Aurinia saxatilis* Golden Alison, *Hirschfeldia incana* Hoary Mustard and *Raphanus sativus* Radish from Cards, on *Cardamine amara* Large Bitter-cress and *Raphanus raphanistrum* subsp. *raphanistrum* Wild Radish from Carms, *Lunaria rediviva* Perennial Honesty from Brecs, *Teesdalia nudicaulis* Shepherd's Cress from Rads, and on *Sinapis arvensis* Charlock and *Hesperis matronalis* Dame's Violet from Caerns. Records of *A. candida* on *Arabidopsis thaliana* Thale Cress from eight vice-counties, where oospores were either not checked or could not be found and so which could not be assigned to either *A. candida* s.s. or *A. laibachii*, must remain *A. candida* s.l. (see the *A. laibachii* description below for distinguishing features). The pustules are mostly white and often cause distortion. Oospores are often not found. At three sites it has been found associated with *Hyaloperonospora*, with *H. nasturtii-aquatici* on *Cardamine flexuosa* at Llanelli, Glam and Llandefaelog, Brecs both in 2019, and with *H. brassicae* on *Brassica oleracea* var. *viridis* Kale in a garden at Aberystwyth, Cards in 2019. Recorded throughout Britain and Ireland. All year.



Albugo candida s.l. on Brassica oleracea var. viridis (left) and var. gemmifera (right)

Albugo candida (Pers.) Roussel s.s.

This is perhaps the most conspicuous mildew dealt with in this book when it heavily infects Capsella bursa-pastoris Shepherd's Purse. The entire above-ground parts of the plant can become contorted and covered in white blisters. It is confined in Wales in the strict sense to Arabis Rock-cresses. Aubrieta Aubretia, Capsella Shepherd'spurses, Erophila Whitlowgrasses and Arabidopsis Thale-cresses, and is certainly under-recorded. It is probably commonest on Capsella bursa-pastoris with records from ten vice-counties, and on Erophila verna Common Whitlowgrass and Arabis caucasica Garden Arabis from three and four repectively. Other records are on Arabis alpina Alpine Rock-cress from Cards, on A. hirsuta Hairy Rock-cress from Carms, on Aubrieta deltoidea Aubretia from Mons and Rads and on *Erophila glabrescens* Glabrous Whitlowgrass from Mons and Angl. Some



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Albugo candida s.s. on Capsella bursapastoris

records on Arabidopsis thaliana Thale Cress from Carms and Cards are confirmed as this species and not A. laibachii as the oospores averaged 48.7µm and 48.4-48.7µm in diameter respectively (see comments also under A. laibachii below). One collection on Capsella bursa-pastoris from an arable field at Plas Gogerddan, Cards in early August 2010, had Hyaloperonospora parasitica mixed with it in the same colonies, a situation which Ingram & Robertson (1999) say often occurs. Oospores are often not found. All year.

Albugo hohenheimia Thines, Ploch & Y.J. Choi (A. candida s.l.)

Common and confined to Cardamine hirsuta Hairy Bittercress. It occurrs on plants in cracks in pavements, on walls and in gardens in ten Welsh vice-counties and will probably prove to be one of our most widespread species. A slight yellowing of the upper leaf surface followed occasionally by a purple discolouration betrays its presence on the lower surface of the leaves as large white blisters. Oospores are rarely found and it is distinguished from A. leimonia by the primary sporangia being significantly smaller than the secondary ones (Thines et al. 2009). Its British distribution is uncertain although there are scattered records throughout Britain and Ireland. All year.



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Albugo hoheneimia on Cardamine hirsuta

Albugo laibachii Thines & Y.J. Choi (A. candida s.l.)

Confined to Arabidopsis thaliana Thale Cress. According to Thines et al. (2009) the oospores are (36.8-)38.3-43.3(-47)µm (average 40.8) in diameter, whereas those of A. candida s.s. on the same host are (42-)45.9-53.0(-55)µm (average 49.5). In spite of a comment by R.W. Michelmore in Spencer (1981, p.178), who, after discussing variation in



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Oospore of Albugo laibachii

Albugo laibachii on Arabidopsis thaliana

oospore size in general in downy mildews, says: "Oospore diameter, therefore, should not be regarded as a definitive taxonomic character" at least in this case the oospore character seems to work as it is confirmed by DNA analysis. Material from five Welsh vice-counties so far checked shows A. laibachii to be present and often common. One Cards collection had oospores ranging from 30-52µm, but averaging 40.9µm (n=13); this is presumably A. laibachii even though some oospores exceed the upper size limit in the description. Material lacking oospores is here recorded as A. candida s.l. Apart from usually a dark, purplish or brownish tinge, the infection is normally not at all obvious when the leaves are seen from above. The pustules on the lower leaf surface are white and oospores are almost always present. March-May.

Albugo leimonia Thines, Ploch & Y.J. Choi (A. candida s.l.)

Confined to Cardamine pratensis Cuckooflower and so far recorded in Wales only from Glam, Rads, Carms, Cards, Caerns and Angl. The pustules are white, with pale or yellowish



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Albugo leimonia on Cardamine pratensis

spots above. It is distinguished morphologically from *A. hohenheimia* by the primary and secondary sporangia being about the same size (Thines *et al.* 2009). Index Fungorum has corrected the specific epithet from the original "*leimonios*" to "*leimonia*". The Rads population was on host plants in deep shade under *Salix cinerea* Grey Willow beside a pond. The distinctive white blisters are produced mostly on the underside of the basal leaves making observation of them difficult and given the relative abundance of the host, often in rank damp vegetation, the mildew may have been overlooked, but does appear to be genuinely rare. Elsewhere there seem to be only three records from England and one from Scotland. May-Oct.

Albugo lepigoni (de Bary) Kuntze

Confined to *Spergula* Spurreys and *Spergularia* Sea-spurreys and only recorded on the latter genus in Wales. It is probably widespread on *S. marina* Lesser Sea-spurrey with records from six vice-counties (see image below) and *S. media* Greater Sea-spurrey from five, all mostly in salt marshes. On *S. rupicola* Rock Sea-spurrey it has been recorded on rock and masonry along much of the Cards coast and from Caerns and Angl and is doubtless more widespread. There is also a single record from *Spergularia rubra* Sand Spurrey, an increasing roadside species, from a road verge in Llanrhystud in Cards. The pustules tend to be slightly yellowish and do not cause significant tissue distortion. It is widely recorded throughout Britain, though it is mostly coastal. Apr-Sept.



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Albugo lepigoni on Spergularia marina



Albugo lepigoni on Spergularia marina

Albugo lepigoni on Spergularia rupicola

Albugo rorippae Y.J. Choi, H.D. Shin, Ploch & Thines (A. candida s.l.)

Occuring only on Rorippa Yellow-cresses, it has been rarely recorded from Wales. It has been found on R. islandica Northern Yellow-cress at Ynys-hir and by the Afon Teifi in Cards and on R. palustris Marsh Yellow-cress once by the Afon Teifi in Cards, once from Brecs



Albugo rorippae on Rorippa islandica

and twice from Carms. The pustules on the lower surface of the leaf are white and there is no distortion of the host. There are very few other records for Britain, but it is doubtless under-recorded. June-Oct.



Albugo rorippae on Rorippa islandica

©AO Chatei

Pustula Thines

Confined to various genera in the Asteraceae Daisy family and Hydrocotylaceae Pennywort family, and confined in Wales to the former. The sporangia are of two types, the first-formed in the chain being sterile, thick-walled and yellowish, and the later-formed are fertile, thin-walled and colourless (Thines & Spring 2005, Constantinescu & Thines 2006).



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Sporangia of *Pustula obtusata* showing thick and thin walls

Pustula obtusata (Link) C. Rost s.l. (Albugo tragopogonis s.l.)



Reported from many genera of Asteraceae Daisy family and in Wales it has been chiefly recorded on Senecio Groundsels with records on S. vulgaris, Groundsel from 12 vice-counties, on *S. sylvaticus* Heath Groundsel and *S.* squalidus Oxford Ragwort from three and S. viscosus Sticky Groundsel from one. Vize (1879) reported it on Matricaria sp. Mayweed from Monts and there are recent records on Scorzonera humilis Viper's-grass from Glams and on Jacobaea vulgaris Common Ragwort from Caerns. The white or yellowish-white crusts are very conspicuous and often cause considerable distortion of the leaves and stems, and the sporangia are all more or less similar in shape. It has been recorded throughout Britain and Ireland, mostly as Albugo tragopogonis. The forms on these genera may be expected to comprise one or more other species. Apr-Dec.

(left) Pustula obtusata s.l. on leaf of Jacobaea vulgaris



Pustula obtusata s.l. on Senecio vulgaris

Pustula obtusata (Link) C. Rost s.s. (Albugo tragopogonis s.l.)

Confined to *Tragopogon* Goat's-beards and only occurring on Tragopogon pratensis ssp. minor Goat'sbeard in Wales. There are recent records from Mons, Glam, Rads, Carms, Pembs, Cards, Caerns and Angl with Vize reporting it from Forden, Monts in 1871. The pustules are white, becoming yellowish (see image right) and there is sometimes considerable deformation of the host. Widely recorded throughout England, often as Albugo or Pustula tragopogonis. May-Sept.

> Pustula obtusata s.s. on Tragopogon pratensis



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Pustula spinulosa (de Bary) Thines (Albugo tragopogonis s.l.)

Confined to Centaurea Knapweeds and Cirsium Thistles and recorded only on the latter from Wales. Reported three times from Cards and four times from Caerns on Cirsium palustre Marsh Thistle. On C. vulgare Spear Thistle there are single records from Cards and Caerns. On C. arvense Creeping Thistle there is a record from Monts in 1873 and recent ones from Caerns, Denbs and Angl. On C. dissectum Meadow Thistle there is a single 1967 record from Kenfig Burrows, Glam. The shiny white or yellowish, blister-like pustules do not cause significant distortion to the leaf and the sporangia are very varied in shape and size (see image right). It is undoubtably under-recorded, being only obvious once the prickly leaves have been turned over. It has been recorded throughout Britain and Ireland, though often as Albugo or Pustula tragopogonis. All year.



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Pustula spinulosa on Cirsium arvense

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Pustula spinulosa on Cirsium palustre

[Wilsoniana Thines

Confined to Amaranthaceae Goosefoot family, Nyctaginaceae Marvel-of-Peru family and Portulacaceae Purslane family. Not yet recorded in Wales, but *W. bliti* has been recorded recently on *Amaranthus* Pigweeds in Cambridgeshire, Dorset and Middlesex. It differs from *Pustula* in having the sporangium wall with short striations rather than with generally reticulate ornamentation, and in pyriform sporangia being usually present (see Thines & Spring 2005).]

Table of hosts and their downy mildews and white blisterrusts in Britain and Ireland

The table below is included as a guide to what has been recorded from Britain and Ireland and should not be used for making reliable determinations. It is essentially a summary of our records for Wales and an attempt at an interpretation and update of the FRDBI records, those in Preece (2002) and those by various other authors and recorders for the rest of Britain and Ireland. We, however, recognise that it is not a complete and accurate checklist for Britain and Ireland but is the best we have been able to achieve from the above sources.

The host genera are placed in alphabetical order. For host/mildew combinations that occur in Wales, the mildew name is in bold.

Host Species

Aconitum Plasmoverna pygmaea s.l.
Aegopodium Plasmopara nivea s.s.
Agastache Peronospora belbahrii
Agrimonia Peronospora agrimoniae
Alchemilla Peronospora alchemillae
Alliaria Albugo candida s.l.

Hyaloperonospora niessliana

Allium Peronospora destructor

Alyssum Albugo candida s.l.

Hyaloperonospora galligenae

Amaranthus Wilsoniana bliti

Anemone **Peronospora anemones**

Plasmopara pygmaea

Angelica Plasmopara angelicae
Anthriscus Plasmopara chaerophylli
Antirrhinum Peronospora antirrhini

Aquilegia **Peronospora sp.**Arabidopsis Albugo candida s.s. **Albugo laibachii**

Hyaloperonospora arabidopsidis

Arabis Albugo candida s.s.
Arenaria Peronospora campestris

Armoracia Albugo candida s.l.

Hyaloperonospora cochleariae

Asperula Peronospora calotheca
Atriplex Peronospora minor
Aubrieta Albugo candida s.s.
Aurinia Albugo candida s.l.

Hyaloperonospora galligena

Barbarea Albugo candida s.l.

Hyaloperonospora barbareae

Bartsia Plasmopara densa

Beta Peronospora schachtii

Blackstonia Peronospora chlorae

Blitum Peronospora boni-henrici

Brassica Albugo candida s.l.

Hyaloperonospora brassicae

Buddleja **Peronospora harriotii**Cakile **Albugo candida s.l.**

Camelina **Hyaloperonospora camelinae**

Campanula Peronospora corollae Capsella **Albugo candida s.s.**

Hyaloperonospora parasitica s.s.

Cardamine Albugo candida s.l.

Albugo hohenheimia Albugo leimonia

Hyaloperonospora dentariae

Hyaloperonospora nasturtii-aquatici

Centaurea
Bremia centaureae s.l.
Centaurium
Peronospora erythraeae
Peronospora centranthi
Peronospora tomentosa
Peronospora conferta
Peronospora paula

Chaerophyllum Plasmopara chaerophylli
Chenopodium Peronospora chenopodii
Chrysosplenium Peronospora chrysosplenii

Cirsium Bremia cirsii

Pustula spinulosa

Clarkia Peronospora arthurii
Cleome Albugo candida s.l.
Cochlearia Albugo candida s.l.

Hyaloperonospora cochleariae

Coincya Albugo candida s.l.
Conium Plasmopara conii

Conopodium Plasmopara nivea s.l.

Crambe Hyaloperonospora parasitica s.s.

Crepis Bremia lactucae s.l.

Pustula obtusata s.l.

Cucumis Pseudoperonospora cubensis

Cymbalaria **Peronospora linariae**Daucus Plasmopara dauci
Delosperma Albugo trianthemi

Dianthus Peronospora dianthicola
Digitalis Peronospora digitalidis

Diplotaxis Albugo candida s.l.

Peronospora diplotaxidis

Dipsacus Peronospora dipsaci

Dorotheanthus **Peronospora mesembryanthemi**

Epilobium Plasmopara epilobii

Erigeron Basidiophora entospora
Erodium Peronospora erodii
Erophila Albugo candida s.s.

Hyaloperonospora praecox

Eruca Albugo candida s.l.
Ervilia **Peronospora ervi**Ervum Peronospora sp.
Erysimum Albugo candida s.l.

Hyaloperonospora cheiranthi

Erythranthe **Peronospora jacksonii**Euphorbia Peronospora cyparissiae
Peronospora euphorbiae

Peronospora valesiacae

Eustoma Plasmopara euphrasiae
Eustoma Peronospora erythraeae

Fallopia Peronospora polygoni-convolvuli

Ficaria
Peronospora ficariae
Foeniculum
Plasmopara mei-foeniculi
Pragaria
Peronospora fragariae
Fumaria
Peronospora affinis
Galium
Peronospora calotheca
Peronospora aparines

Peronospora aparines Peronospora galii

Geranium Peronospora conglomerate

Plasmopara pusilla

Gerbera Pustula obtusata s.l.
Geum **Peronospora gei**Glebionis Peronospora radii

Glycine Peronospora manshurica
Helianthemum Peronospora leptoclada
Helichrysum Pustula obtusata s.l.

Helleborus Peronospora pulverulacea
Heracleum Plasmopara crustosa s.s.
Hesperis Albugo candida s.l.

Hyaloperonospora hesperidis

Hieracium Bremia lactucae s.l.
Hirschfeldia Albugo candida s.l.

Hyaloperonospora erucastri

Honckenya
Peronospora honckenyae
Hornungia
Hyaloperonospora parasitica s.s.
Humulus
Pseudoperonospora humuli

Hyoscyamus Peronospora hyoscyami
Iberis Peronospora iberidis
Impatiens Plasmopara obducens
Inula Pustula obtusata s.l.

Isopyrum Plasmoverna isopyri-thalictroidis

Jacobaea Bremia tulasnei

Pustula obtusata s.l.

Knautia Peronospora knautiae

Peronospora violacea

Laburnum Peronospora cytisi
Lactuca Bremia lactucae s.s.
Lamiastrum Peronospora lamii
Lamium Peronospora lamii
Lampranthus Albugo trianthemi
Lapsana Bremia lapsanae
Lathyrus Peronospora fulva

Peronospora pisi

Peronospora senneniana Peronospora viciae s.l.

Lepidium Albugo lepidii

Perofascia lepidii

Leucanthemum Peronospora radii
Levisticum Plasmopara nivea s.l.
Ligusticum Plasmopara nivea s.l.
Limonium Peronospora statices
Linaria Peronospora flava
Linum Peronospora lini

Lipandra Peronospora chenopodii-polyspermi

Lisianthus Peronospora erythraeae Lobularia Albugo candida s.l.

Hyaloperonospora lobulariae

Lotus **Peronospora lotorum**

Lunaria Hyaloperonospora lunariae

Albugo candida s.l.

Matricaria Paraperonospora leptosperma

Peronospora radii Pustula obtusata s.l.

Matthiola Albugo candida s.l.

Peronospora matthiolae

Meconopsis Peronospora meconopsidis

Medicago Peronospora aestivalis

Peronospora romanica

MelilotusPeronospora melilotiMenthaPeronospora stigmaticolaMeumPlasmopara mei-foeniculiMisopatesPeronospora antirrhiniMoehringiaPeronospora arenariaeMyosotisPeronospora myosotidisMyrrhisPlasmopara nivea s.l.

Nasturtium **Hyaloperonospora nasturtii-aquatici**

Nicotiana Peronospora tabacina

Noccaea Albugo candida s.l.

Odontites
Plasmopara densa
Oenanthe
Plasmopara nivea s.l.
Oenothera
Peronospora arthurii
Ononis
Peronospora ononidis
Ornithopus
Peronospora ornithopi
Oxybasis
Peronospora chenopodii
Papaver
Peronospora arborescens s.l.

Peronospora meconopsidis Peronospora somnifera

Pastinaca Plasmopara pastinacae

Pericallis
Pustula obtusata s.l.
Petroselinum
Plasmopara petroselini
Phlox
Peronospora phlogina
Picris
Bremia lactucae s.l.
Pilosella
Bremia lactucae s.l.

Plantago **Peronospora alta**

Pimpinella

Polygonum Peronospora polygoni

Potentilla Peronospora potentillae-reptantis

Peronospora potentillae-sterilis

Poterium Peronospora sanguisorbae
Primula **Peronospora oerteliana**Prunus **Peronospora sparsa**Ranunculus Peronospora hiemalis

Peronospora ranunculi

Plasmopara pimpinellae

Raphanus Albugo candida s.l.

Hyaloperonospora brassicae s.l.

Reseda Peronospora crispula
Rheum Peronospora jaapiana
Rhinanthus Plasmopara densa
Ribes Plasmopara ribicola
Rorippa Albugo rorippae

Hyaloperonospora rorippae-islandicae

Rosa Peronospora sparsa
Rubus Peronospora rubi
Rumex Peronospora rumicis
Sanguisorba Peronospora sanguisorbae
Sanicula Plasmopara saniculae
Scabiosa Peronospora violacea
Scleranthus Peronospora scleranthi

Scorzonera **Pustula obtusata s.l.**Scorzoneroides Bremia lactucae s.l.

Scrophularia **Peronospora sordida**Senecio **Bremia tulasnei**

Pustula obtusata s.l.

Sherardia **Peronospora sherardii**

Silene Peronospora melandryi

Sinapis Albugo candida s.l.

Hyaloperonospora brassicae s.l.

Albugo candida s.l. Sisymbrium

Hyaloperonospora sisymbrii-loeselii

Smyrnium Plasmopara nivea s.l. Sonchus Bremia sonchicola Spergula Peronospora obovata

Spergularia Albugo lepigoni Spinacia Peronospora effusa Stachys Peronospora stachydis Stellaria Peronospora alsinearum

Peronospora parva

Albugo candida s.l.

Suaeda Peronospora sp.

Thlaspi

Succisa Peronospora violacea Symphytum Peronospora symphyti Tanacetum Pustula obtusata s.l. **Taraxacum** Bremia taraxaci Teesdalia Albugo candida s.l.

Hyaloperonospora thlaspeos-arvensis

Thysselinum Plasmopara peucedani Tragopogon Pustula obtusata s.s.

Trifolium Peronospora trifolii-arvensis

> Peronospora trifolii-hybridi Peronospora trifoliorum s.l.

Trigonella Peronospora trigonellae

Tripleurospermum Peronospora radii

Paraperonospora leptosperma

Urtica Peronospora debaryi

Pseudoperonospora urticae

Valeriana Peronospora valerianae Valerianella Peronospora valerianellae

Verbascum Peronospora verbasci Verbena Peronospora verbenae Veronica Peronospora agrestis Peronospora arvensis Peronospora grisea

Peronospora fabae

Vicia Peronospora mayorii

Peronospora sepium Peronospora viciae

Viola Peronospora violae Vitis Plasmopara viticola

Census Catalogue

The box below provides a list of Welsh vice-counties (see Watson, 1883 for details), their abbreviations and the numbering system used in the catalogues.

35 41 42 43 44	Monmouthshire Mons Glamorgan Glam Breconshire Brecs Radnorshire Rads Carmarthenshire Carms	47 48 49 50 51	Montgomeryshire Monts Merionethshire Mer Caernarvonshire Caerns Denbighshire Denbs Flintshire Flints
		_	
45 46	Pembrokeshire Pembs Cardiganshire Cards	52	Anglesey Angl

Tabulated below alphabetically by both hosts and mildew (p123) are records from the thirteen vice-counties of Wales. Vice-county numbers in square brackets are based on records made pre-1970. We have attempted to indicate the status of individual plants of the hosts infected in Wales as follows: **native** bold; *archaeophyte* italic; <u>neophyte</u> or <u>naturalised</u> underlined; casual or cultivated normal font.

Host	Downy mildew/bilster-rust	Distribution
Aegopodium podagraria	Plasmopara nivea s.s.	35, 41, 42, 43, 44,
		45, 46, 47, 48,
		49, 50, 52
Agrimonia sp.	Peronospora agrimoniae	43
Alliaria petiolata	Hyaloperonospora niessleana	35, 42, 43, 44, 45,
		46, 47, 49, 50,
		51, 52
Allium cepa	Peronospora destructor	[41], [42], [44], [45], [46], [48], 49, [50]
Allium ursinum	Peronospora destructor	[50]
Anemone coronaria	Peronospora anemones	[35], [45], [46], [49]
	Plasmoverna pygmaea	[45], [46]
Anemone nemorosa	Plasmoverna pygmaea	35, 42, 43, 44, 45,
		46, 47, 48, 49,
		50, 51, 52
Angelica sylvestris	Plasmopara angelicae	41, 42, 43, 44, 45,
		46, 48, 49, 50,
		51, 52
Anthriscus sylvestris	Plasmopara chaerophylli	35, 44, 46, 49, 50,
		[51], 52
Antirrhinum majus	Peronospora antirrhini	[35], [44], [46], [49]
Aquilegia vulgaris	Peronospora sp.	41, 42, 44
Arabidopsis thaliana	Albugo candida s.l.	35, 42, 43, 44, 47,
		48, 49, 50
	Albugo candida s.s.	44, 46
	Albugo laibachii	42, 46, 47, 48, 49
	Hyaloperonospora	44, 46
	arabidopsidis	

Host	Downy mildew/bilster-rust	Distribution
Arabis alpina	Albugo candida s.s.	46
Arabis caucasica	Albugo candida s.s.	43, 45, 46, 50
Arabis hirsuta	Albugo candida s.s.	44
Atriplex patula	Peronospora minor	46, 48, 49, 52
Atriplex prostrata	Peronospora minor	46, 49, 50, 52
Aubrieta deltoidea	Albugo candida s.s.	43, 35
Aurinia saxatilis	Albugo candida s.l.	46
	Hyaloperonospora galligena	[41], 51
Barbarea verna	Albugo candida s.l.	46, 49
	Hyaloperonospora barbareae	46, 49
Beta vulgaris ssp. maritima	Peronospora schachtii	49, 52
Beta vulgaris ssp. vulgaris	Peronospora schachtii	[46]
Blitum bonus-henricus	Peronospora boni-henrici	35, 52
Brassica cv.	Hyaloperonospora brassicae	42
Brassica napus	Hyaloperonospora brassicae	[35], [46], [49], 50
Brassica oleracea	Hyaloperonospora brassicae	35, [41], [47], 50,
	, . ,	[51]
Brassica oleracea var. botrytis	Albugo candida s.l.	46, 49
Brassica oleracea var. capitata	Albugo candida s.l.	49
Brassica oleracea var. gemmifera	Albugo candida s.l.	46
Brassica oleracea var. viridis	Albugo candida s.l.	46
	Hyaloperonospora brassicae	46
Brassica rapa ssp. campestris	Albugo candida s.l.	46, 49, 52
, , ,	Hyaloperonospora brassicae	49
Buddleja davidii	Peronospora hariotii	45, 48, 49, 52
Cakile maritima	Albugo candida s.l.	49, 52
Camelina microcarpa	Hyaloperonospora camelinae	49
Capsella bursa-pastoris	Albugo candida s.s.	35, 41, 42, 43, 44,
		45, 46, 47, 49, 52
	Hyaloperonospora parasitica	42, 44, 46, 49
	S.S.	
Cardamine amara	Albugo candida s.l.	44
Cardamine flexuosa	Albugo candida s.l.	35, 41, 42, 44, 45,
		46, 48, 49, 50, 52
	Hyaloperonospora nasturtii-	41, 42, 43, 44, 46,
	aquatici	49
Cardamine hirsuta	Albugo hohenheimia	42, 43, 44, 45, 46,
		47, 48, 49, 52
	Hyaloperonospora nasturtii-	35, 42, 43, 44, 45, 46
	aquatici	
Cardamine pratensis	Albugo leimonia	41, 43, 44, 46, 49, 52
	Hyaloperonospora nasturtii-	44
	aquatici	
Centaurea nigra	Bremia centaureae	44, 46, 48, 49
Centaurium erythraea	Peronospora erythraeae	43, 44, 46

Host	Downy mildew/bilster-rust	Distribution
Cerastium fontanum ssp.	Peronospora conferta	42, 43, 44, 45, 46,
vulgare .	·	47, 49, 51, 52
	Peronospora paula	35, 44,46
Cerastium glomeratum	Peronospora conferta	35, 46
_	Peronospora tomentosa	35, 42, 43, 44, 46,
	·	47, 49, 52
Cerastium sp.	Peronospora conferta	[45]
Chenopodium album	Peronospora chenopodii	42, 43, 44, 45, 46,
-		49, 50, 51, 52
Chenopodium ficifolium	Peronospora chenopodii	44, 46
Cirsium arvense	Pustula spinulosa	[47], 49, 50, 52
Cirsium palustre	Bremia cirsii	49
	Pustula spinulosa	46, 49
Cirsium vulgare	Bremia cirsii	43, 46, 49, 52
_	Pustula spinulosa	46, 49
Cochlearia danica	Albugo candida s.l.	44, 46
	Hyaloperonospora cochleariae	52
Cochlearia officinalis	Albugo candida s.l.	44, 46, 49, 52
	Hyaloperonospora cochleariae	46
Conopodium majus	Plasmopara nivea s.l.	42, 43, 44, 45, 46,
		47, 48, 49, 50, 52
Crambe maritima	Hyaloperonospora parasitica	[41]
	s.s.	
Crepis capillaris	Bremia lactucae s.l.	49
Cymbalaria muralis	Peronospora linariae	[49]
Digitalis purpurea	Peronospora digitalidis	49, 51, 52
Dipsacus fullonum	Peronospora dipsaci	41, 43, 44
Dorotheanthus bellidiformis	Peronospora	[35]
	mesembryanthemi	
Epilobium sp.	Plasmopara epilobii	49
Erophila glabrescens	Albugo candida s.s.	35, 52
Erophila verna	Albugo candida s.s.	42, 43, 46, 47
	Hyaloperonospora praecox	47
Ervilia hirsuta	Peronospora ervi	41, 42, 43, 45, 46,
		49, 52
Erysimum cheiri	Hyaloperonospora cheiranthi	43, 46, 49
Erythranthe sp.	Peronospora jacksonii	35
Euphrasia arctica ssp. borealis	Plasmopara euphrasiae	44
Euphrasia confusa × nemorosa	Plasmopara euphrasiae	44, 46
Euphrasia confusa × tetraquetra	Plasmopara euphrasiae	46
Euphrasia nemorosa	Plasmopara euphrasiae	46
Euphrasia officinalis agg.	Plasmopara euphrasiae	35, 48
Euphrasia officinalis ssp.	Plasmopara euphrasiae	46
anglica		
Euphrasia officinalis ssp.	Plasmopara euphrasiae	44
pratensis		40.40
Euphrasia sp.	Plasmopara euphrasiae	48, 49

Host	Downy mildew/bilster-rust	Distribution
Ficaria verna	Peronospora ficariae	51, 52
Ficaria verna ssp. fertilis	Peronospora ficariae	35, 41, 42, 43, 44,
	·	45, 46, 47, 48,
		49, 50
Ficaria verna ssp. verna	Peronospora ficariae	42, 43, 46, 47, 48
Fumaria bastardii var. bastardii	Peronospora affinis	45, 46, 49
Fumaria muralis ssp. boraei	Peronospora affinis	42, 43, 45, 46, 49,
Tumana marana 33p. boraci	l oronospora amino	50
Fumaria officinalis	Peronospora affinis	43, 44, 45, 49, 52
Fumaria officinalis ssp. officinalis	Peronospora affinis	44, 46
Fumaria officinalis ssp. wirtgenii	Peronospora affinis	46
Fumaria sp.	Peronospora affinis	[49]
Galium aparine	Peronospora aparines	35, 42, 43, 44, 45,
	Peronospora aparines	46, 47, 49, 50,
Galium odoratum	Poroposporo colothogo	51, 52 42, 43, 46, 47, 48,
Ganum odoratum	Peronospora calotheca	
Colium poluotro	Derencenera galii	49, 50
Galium palustre Galium saxatile	Peronospora galii	46, 49, 52
	Peronospora galii	46
Galium verum	Peronospora galii	46
Geranium dissectum	Peronospora conglomerata	44, 46, 49
Geranium lucidum	Peronospora conglomerata	46, 49
Geranium molle	Peronospora conglomerata	46, 49, 52
Geranium pratense	Plasmopara pusilla s.s.	[43], 52
Geranium pyrenaicum	Peronospora conglomerata	44, 52
	Plasmopara pusilla s.l.	51, 52
Geranium robertianum	Peronospora conglomerata	46
Geranium sylvaticum	Plasmopara pusilla s.l.	[42]
Geum urbanum	Peronospora gei	50
<u>Hesperis matronalis</u>	Albugo candida s.l.	49
	Hyaloperonospora hesperidis	42
Hieracium sp.	Bremia lactucae s.l.	49
<u>Hirschfeldia incana</u>	Albugo candida s.l.	46
	Hyaloperonospora erucastri	46
Honckenya peploides	Peronospora honckenyae	44
Humulus lupulus	Pseudoperonospora humuli	35, 42, 43, 44, 46
Impatiens walleriana	Plasmopara obducens	35, 46
Jacobaea vulgaris	Bremia tulasnei	44, 49
	Pustula obtusata s.l.	49
Lactuca sativa	Bremia lactucae s.s.	35, [41], [43], [44],
		45, 46, [47], 49,
		50, [52]
Lamium maculatum	Peronospora lamii	[47], 52
Lamium purpureum	Peronospora lamii	42
Lapsana communis ssp.	Bremia lapsanae	42, 43, 44, 46, [47],
communis		50, 51

Host	Downy mildew/bilster-rust	Distribution
Lathyrus nissolia	Peronospora fulva	35
Lathyrus odoratus	Peronospora viciae s.l.	[45], [46], [48]
Lathyrus oleraceus	Peronospora pisi	[35], [41], [47]
Lathyrus sylvestris	Peronospora senneniana	44
Lepidium coronopus	Perofascia lepidii	46
Lepidium didymum	Perofascia lepidii	46
Ligusticum scoticum	Plasmopara nivea s.l.	46
Linaria purpurea	Peronospora flava	46
Linaria vulgaris	Peronospora flava	45, 46
Lobularia maritima	Albugo candida s.l.	42, 46, 49
	Hyaloperonospora lobulariae	41, 49
Lotus corniculatus	Peronospora lotorum	44, 49
Lotus pedunculatus	Peronospora lotorum	35, 43, 44, 45, 46, 47, 52
Lunaria annua	Albugo candida s.l.	35, 41, 42, 43, 46, 49, 52
Lunaria rediviva	Albugo candida s.l.	42
Matricaria chamomilla	Paraperonospora leptosperma s.l.	43, 49, 52
Matricaria discoidea	Paraperonospora leptosperma s.l.	43, 46
Matricaria sp.	Pustula obtusata s.l.	[47]
Meconopsis betonicifolia	Peronospora meconopsidis	[47]
Medicago lupulina	Peronospora romanica	41, 43, 44, 45, [47], 50
Medicago sativa	Peronospora aestivalis	[41], 44
Melilotus altissimus	Peronospora meliloti	44
Melilotus officinalis	Peronospora meliloti	44
Misopates orontium	Peronospora antirrhini	44
Moehringia trinervia	Peronospora arenariae	44, 46, [47], 51
Myosotis sylvatica	Peronospora myosotidis	46, 49
Nasturtium officinale	Hyaloperonospora nasturtii- aquatici	42
Nicotiana cv.	Peronospora tabacina	45
Nicotiana sylvestris cv.	Peronospora tabacina	49
Nicotiana tabacum	Peronospora tabacina	49, 52
Odontites vernus	Plasmopara densa	41, 43, 44, 46, [47], 49, 51, 52
Odontites vernus ssp.	Plasmopara densa	44
serotinus		
Oenanthe crocata	Plasmopara nivea s.l.	35, 42, 43, 44, 46, 49
Ononis repens	Peronospora ononidis	46
Ornithopus perpusillus	Peronospora ornithopi	49
Oxybasis rubrum	Peronospora chenopodii	35

Host	Downy mildew/bilster-rust	Distribution
Papaver cambricum	Peronospora meconopsidis	41, 42, 43, 44, 46,
		47, 48, 49, 50, 51
Papaver dubium	Peronospora arborescens s.l.	52
Papaver setiferum	Peronospora arborescens s.l.	46
Papaver somniferum	Peronospora meconopsidis	42, 43, 46, 49
Pastinaca sativa	Plasmopara pastinacae	[41]
Phlox sp.	Peronospora phlogina	[46]
Pilosella aurantiaca ssp.	Bremia lactucae s.l.	43, 46, 49
<u>carpathicola</u>		
Pimpinella saxifraga ssp.	Plasmopara pimpinellae	42, 46
saxifraga		
Plantago lanceolata	Peronospora alta	[51]
Plantago major ssp. major	Peronospora alta	35, 41, 42, 43, 44,
		46, 49, 50, 51
Polygonum aviculare	Peronospora polygoni	49, 52
Potentilla reptans	Peronospora potentillae-	41, 49, 51
	reptantis	
Potentilla sterilis	Peronospora potentillae-sterilis	43, 44, 46
Primula veris	Peronospora oerteliana	[50]
Primula vulgaris	Peronospora oerteliana	35, 42, 44, [47], [48], 51
Prunus laurocerasus	Peronospora sparsa	41
Ranunculus acris	Peronospora ranunculi	44, 46, 49, 52
Ranunculus bulbosus	Peronospora ranunculi	35, 44, 46, 49
Ranunculus flammula	Peronospora ranunculi	35, 43, 46, 47, 49
Ranunculus repens	Peronospora ranunculi	35, 42, 43, 45, 46,
		47, 48, 49, 50,
		51, 52
Raphanus raphanistrum ssp.	Albugo candida s.l.	41, 44, 49, 52
maritimus		
Raphanus raphanistrum ssp.	Albugo candida s.l.	44
raphanistrum		
Raphanus sativus	Albugo candida s.l.	46
Reseda luteola	Peronospora crispula	46, 49
Rhinanthus minor	Plasmopara densa	42, 43, 44, 46, [47], 48, 49, 50, 51, 52
Rorippa islandica	Albugo rorippae	46
	Hyaloperonospora rorippae- islandicae	42, [46]
Rorippa palustris	Albugo rorippae	42, 44, 46
	Hyaloperonospora rorippae-	42, 46
Deep ev	islandicae	40
Rosa cv.	Peronospora sparsa	49
Rubus fruticosus agg.	Peronospora rubi	41, 42, 43, 49, 52
Rubus fruticosus agg. × idaeus	Peronospora rubi	49
Rubus idaeus	Peronospora rubi	51
Rumex acetosa ssp. acetosa	Peronospora rumicis	43, 45, 46

Host	Downy mildew/bilster-rust	Distribution
Sanicula europaea	Plasmopara saniculae	[47]
Scorzonera humilis	Pustula obtusata s.l.	41
Scrophularia auriculata	Peronospora sordida	46
Scrophularia nodosa	Peronospora sordida	[43], 44, 46, [47],
•	·	[48], 49, 50, 51,
		52
Senecio squalidus	Pustula obtusata s.l.	44, 49, 52
Senecio sylvaticus	Pustula obtusata s.l.	46, 49, 52
Senecio viscosus	Pustula obtusata s.l.	43
Senecio vulgaris	Bremia tulasnei	43, [47], [48], 49
	Pustula obtusata s.l.	35, 41, 42, 43, 44,
		45, 46, 47, 48,
		49, 51, 52
Sherardia arvensis	Peronospora sherardii	46
Silene dioica	Peronospora melandryi	52
Sinapis arvensis	Albugo candida s.l.	49
Chiapis an consis	Hyaloperonospora brassicae	49
Sisymbrium officinale	Albugo candida s.l.	44, 46, 49, 50, 52
Giogniam omenaie	Hyaloperonospora sisymbrii-	43, 45, 46, 47, 49,
	loeselii	50, 51
Smyrnium olusatrum	Plasmopara nivea s.l.	49, 52
Sonchus asper	Bremia sonchicola	35, 42, [43], 46, 47,
Concilus asper	Bremia seriemocia	49, 52
Sonchus oleraceus	Bremia sonchicola	43, 49
Spergula arvensis	Peronospora obovata	46, 49
Spergularia marina	Albugo lepigoni	35, 41, 44, 46, 49, 52
Spergularia media	Albugo lepigoni	44, 46, 48, 49, 52
Spergularia rubra	Albugo lepigoni	46
Spergularia rupicola	Albugo lepigoni	46, 49, 52
Spergularia sp.	Albugo lepigoni	48, 49, 52
Spinacea oleracea	Peronospora effusa	[47]
Stachys arvensis	Peronospora stachydis	50
Stellaria alsine	Peronospora parva	49, 52
Stellaria graminea	Peronospora parva	49
Stellaria media	Peronospora alsinearum	44, 45, 46, [47], 49,
	-	52
Stellaria pallida	Peronospora parva	46
Suaeda maritima	Peronospora sp.	52
Succisa pratensis	Peronospora violacea	35, 42, 43, 45, 46, 48
Symphytum officinale	Peronospora symphyti	51
Taraxacum sp.	Bremia taraxaci	46
Teesdalia nudicaulis	Albugo candida s.l.	43
Tragopogon pratensis ssp.	Pustula obtusata s.s.	35, 41, 43, 44, 45,
minor		46, [47], 49, 52

Host	Downy mildew/bilster-rust	Distribution
Trifolium dubium	Peronospora trifolii-arvensis	35, 42, 43, 44, 51
Trifolium hybridum	Peronospora trifolii-hybridi	[50]
Trifolium medium	Peronospora trifoliorum s.l.	43, 51
Trifolium pratense	Peronospora trifolii-hybridi	42, 46
Trifolium repens	Peronospora trifoliorum s.l.	43, 51
Trifolium sp.	Peronospora trifoliorum s.l.	[47]
Tripleurospermum inodorum	Paraperonospora leptosperma	46
Tripleurospermum maritimum	Paraperonospora leptosperma	46, 52
ssp. maritimum	s.l.	.0,02
Urtica dioica	Pseudoperonospra urticae	35, 41, 46, [47], 51
Valeriana officinalis	Peronospora valerianae	49, 52
Valerianella carinata	Peronospora valerianellae	46
Valerianella locusta	Peronospora valerianellae	46
Verbena officinalis	Peronospora verbenae	44, 46
Veronica agrestis	Peronospora agrestis	43
Veronica arvensis	Peronospora agrestis	43, 46
Veronica beccabunga	Peronospora grisea	42, 44, 45, 46, [47], 48, 49, 50
Veronica chamaedrys	Peronospora agrestis	46
<u>Veronica filiformis</u>	Peronospora agrestis	41
Veronica hederifolia	Peronospora arvensis	42, 43, 44, 45, 46, 47, 48, 49, 50
Veronica hederifolia ssp. lucorum	Peronospora arvensis	43, 44
Veronica montana	Peronospora grisea	35, 44
<u>Veronica persica</u>	Peronospora agrestis	45, 49
Veronica serpyllifolia	Peronospora grisea	35, 43, 44, 45, 46, 47, 48, 49, 50, 52
Veronica subgen.	Peronospora grisea	48, 49, 52
Pseudoveronica (Hebe) sp.		
Vicia cracca	Peronospora mayorii	49
Vicia lathyroides	Peronospora viciae	46
Vicia orobus	Peronospora viciae s.l.	43
Vicia sativa	Peronospora viciae	44
Vicia sativa ssp. nigra	Peronospora viciae	43, 45, 46, 49, 52
Vicia sativa ssp. segetalis	Peronospora viciae	41, 42, 43, 44, 45, 46, 47, 49, 52
Vicia sepium	Peronospora sepium	35, 42, 43, 44, 46, 49, 50, 51
Viola arvensis	Peronospora violae	43, 44, 46, 50
Viola riviniana	Peronospora violae	44
Viola sp.	Peronospora violae	[47]
Vitis vinifera	Plasmopara viticola	35
Vitis vinifera 'Purpurea'	Plasmopara viticola	47

Downy mildew/bilster-rust	Host	Distribution
Albugo candida s.l.	Arabidopsis thaliana	35, 42, 43, 44, 47,
		48, 49, 50
	Aurinia saxatilis	46
	Barbarea verna	46, 49
	Brassica oleracea var. botrytis	46, 49
	Brassica oleracea var. capitata	49
	Brassica oleracea var. gemmifera	46
	Brassica oleracea var. viridis	46
	Brassica rapa ssp. campestris	46, 49, 52
	Cakile maritima	49, 52
	Cardamine amara	44
	Cardamine flexuosa	35, 41, 42, 44, 45, 46, 48, 49, 50, 52
	Cochlearia danica	44, 46
	Cochlearia officinalis	44, 46, 49, 52
	Hesperis matronalis	49
	Hirschfeldia incana	46
	Lobularia maritima	42, 46, 49
	<u>Lunaria annua</u>	35, 41, 42, 43, 46, 49, 52
	Lunaria rediviva	42
	Raphanus raphanistrum ssp. maritimus	41, 44, 49, 52
	Raphanus raphanistrum ssp. raphanistrum	44
	Raphanus sativus	46
	Sinapis arvensis	49
	Sisymbrium officinale	44, 46, 49, 50, 52
	Teesdalia nudicaulis	43
Albugo candida s.s.	Arabidopsis thaliana	44, 46
	Arabis alpina	46
	Arabis caucasica	43, 45, 46, 50
	Arabis hirsuta	44
	Aubrieta deltoidea	43, 35
	Capsella bursa-pastoris	35, 41, 42, 43, 44,
		45, 46, 47, 49, 52
	Erophila glabrescens	35, 52
	Erophila verna	42, 43, 46, 47
Albugo hohenheimia	Cardamine hirsuta	42, 43, 44, 45, 46,
		47, 48, 49, 52
Albugo laibachii	Arabidopsis thaliana	42, 46, 47, 48, 49
Albugo leimonia	Cardamine pratensis	41, 43, 44, 46, 49, 52

Downy mildew/bilster-rust	Host	Distribution
Albugo lepigoni	Spergularia marina	35, 41, 44, 46, 49, 52
	Spergularia media	44, 46, 48, 49, 52
	Spergularia rubra	46
	Spergularia rupicola	46, 49, 52
	Spergularia sp.	48, 49, 52
Albugo rorippae	Rorippa islandica	46
	Rorippa palustris	42, 44, 46
Bremia centaureae	Centaurea nigra	44, 46, 48, 49
Bremia cirsii	Cirsium palustre	49
	Cirsium vulgare	43, 46, 49, 52
Bremia lactucae s.l.	Crepis capillaris	49
	Hieracium sp.	49
	Pilosella aurantiaca ssp.	43, 46, 49
	<u>carpathicola</u>	
Bremia lactucae s.s.	Lactuca sativa	35, [41], [43], [44],
		45, 46, [47], 49,
		50, [52]
Bremia lapsanae	Lapsana communis ssp.	42, 43, 44, 46, [47],
Bremia sonchicola	communis	50, 51
bremia sonchicola	Sonchus asper	35, 42, [43], 46, 47, 49, 52
	Sonchus oleraceus	43, 49
Bremia taraxaci	Taraxacum sp.	46
Bremia tulasnei	Jacobaea vulgaris	44, 49
	Senecio vulgaris	43, [47], [48], 49
Hyaloperonospora arabidopsidis	Arabidopsis thaliana	44, 46
Hyaloperonospora barbareae	Barbarea verna	46, 49
Hyaloperonospora brassicae	Brassica cv.	42
	Brassica napus	[35], [46], [49], 50
	Brassica oleracea	35, [41], [47], 50, [51]
	Brassica oleracea var. viridis	46
	Brassica rapa ssp. campestris	49
	Sinapis arvensis	49
Hyaloperonospora camelinae	Camelina microcarpa	49
Hyaloperonospora cheiranthi	Erysimum cheiri	43, 46, 49
Hyaloperonospora cochleariae	Cochlearia danica	52
	Cochlearia officinalis	46
Hyaloperonospora erucastri	<u>Hirschfeldia incana</u>	46
Hyaloperonospora galligena	Aurinia saxatilis	[41], 51
Hyaloperonospora hesperidis	Hesperis matronalis	42
Hyaloperonospora lobulariae	<u>Lobularia maritima</u>	41, 49

Downy mildew/bilster-rust Hyaloperonospora nasturtii- aquatici	Cardamine flexuosa	
aquatici	Cardannine nexuosa	41, 42, 43, 44, 46, 49
	Cardamine hirsuta	35, 42, 43, 44, 45, 46
	Cardamine pratensis	44
	Nasturtium officinale	42
Hyaloperonospora niessleana	Alliaria petiolata	35, 42, 43, 44, 45,
		46, 47, 49, 50,
		51, 52
Hyaloperonospora parasitica	Capsella bursa-pastoris	42, 44, 46, 49
S.S.	Out make a managiti mana	[44]
Uhvelen enen een en ene	Crambe maritima	[41]
Hyaloperonospora praecox	Erophila verna	47
Hyaloperonospora rorippae- islandicae	Rorippa islandica	42, [46]
isianticae	Rorippa palustris	42, 46
Hyaloperonospora sisymbrii-	Sisymbrium officinale	43, 45, 46, 47, 49,
loeselii	Gloymonam omomate	50, 51
Paraperonospora leptosperma	Matricaria chamomilla	43, 49, 52
s.l.		
	Matricaria discoidea	43, 46
	Tripleurospermum inodorum	46
	Tripleurospermum maritimum	46, 52
	ssp. maritimum	
Perofascia lepidii	Lepidium coronopus	46
	<u>Lepidium didymum</u>	46
Peronospora aestivalis	Medicago sativa	[41], 44
Peronospora affinis	Fumaria bastardii var. bastardii	45, 46, 49
	Fumaria muralis ssp. boraei	42, 43, 45, 46, 49, 50
	Fumaria officinalis	43, 44, 45, 49, 52
	Fumaria officinalis ssp. officinalis	44, 46
	Fumaria officinalis ssp. wirtgenii	46
	Fumaria sp.	[49]
Peronospora agrestis	Veronica agrestis	43
	Veronica arvensis	43, 46
	Veronica chamaedrys	46
		· ·
	-	
Peronospora alsinearum	Stellaria media	
Peronosnora alta	Plantago lancoolata	
רפוטווטאטומ מונמ		• · ·
	i lantago major ssp. major	46, 49, 50, 51
Peronospora anemones	Anemone coronaria	[35], [45], [46], [49]
Peronospora agrimoniae Peronospora alsinearum Peronospora alta	Veronica chamaedrys Veronica filiformis Veronica persica Agrimonia sp. Stellaria media Plantago lanceolata Plantago major ssp. major	41 45, 49 43 44, 45, 46, [47], 49, 52 [51] 35, 41, 42, 43, 44,

Downy mildew/bilster-rust	Host	Distribution
Peronospora antirrhini	Antirrhinum majus	[35], [44], [46], [49]
-	Misopates orontium	44
Peronospora aparines	Galium aparine	35, 42, 43, 44, 45,
	·	46, 47, 49, 50,
		51, 52
Peronospora arborescens s.l.	Papaver dubium	52
	Papaver setiferum	46
Peronospora arenariae	Moehringia trinervia	44, 46, [47], 51
Peronospora arvensis	Veronica hederifolia	42, 43, 44, 45, 46,
		47, 48, 49, 50
	Veronica hederifolia ssp. lucorum	43, 44
Peronospora boni-henrici	Blitum bonus-henricus	35, 52
Peronospora calotheca	Galium odoratum	42, 43, 46, 47, 48,
		49, 50
Peronospora chenopodii	Chenopodium album	42, 43, 44, 45, 46,
		49, 50, 51, 52
	Chenopodium ficifolium	44, 46
	Oxybasis rubrum	35
Peronospora conferta	Cerastium fontanum ssp.	42, 43, 44, 45, 46,
	vulgare	47, 49, 51, 52
	Cerastium glomeratum	35, 46
	Cerastium sp.	[45]
Peronospora conglomerata	Geranium dissectum	44, 46, 49
	Geranium lucidum	46, 49
	Geranium molle	46, 49, 52
	Geranium pyrenaicum	44, 52
	Geranium robertianum	46
Peronospora crispula	Reseda luteola	46, 49
Peronospora destructor	Allium cepa	[41], [42], [44], [45],
		[46], [48], 49, [50]
	Allium ursinum	[50]
Peronospora digitalidis	Digitalis purpurea	49, 51, 52
Peronospora dipsaci	Dipsacus fullonum	41, 43, 44
Peronospora effusa	Spinacea oleracea	[47]
Peronospora ervi	Ervilia hirsuta	41, 42, 43, 45, 46,
		49, 52
Peronospora erythraeae	Centaurium erythraea	43, 44, 46
Peronospora ficariae	Ficaria verna	51, 52
	Ficaria verna ssp. fertilis	35, 41, 42, 43, 44,
		45, 46, 47, 48,
	Figaria vorna sen vorna	49, 50 42, 43, 46, 47, 48
Poronospora flova	Ficaria verna ssp. verna	42, 43, 46, 47, 46
Peronospora flava	Linaria purpurea	45, 46
Doronognoro fulvo	Linaria vulgaris	·
Peronospora fulva	Lathyrus nissolia	35

Downy mildew/bilster-rust	Host	Distribution
Peronospora galii	Galium palustre	46, 49, 52
	Galium saxatile	46
	Galium verum	46
Peronospora gei	Geum urbanum	50
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Peronospora grisea	Veronica beccabunga	42, 44, 45, 46, [47], 48, 49, 50
	Veronica montana	35, 44
	Veronica serpyllifolia	35, 43, 44, 45, 46, 47, 48, 49, 50, 52
	Veronica subgen.	48, 49, 52
	Pseudoveronica (Hebe) sp.	, ,
Peronospora hariotii	Buddleja davidii	45, 48, 49, 52
Peronospora honckenyae	Honckenya peploides	44
·	Erythranthe sp.	35
Peronospora jacksonii		
Peronospora lamii	<u>Lamium maculatum</u>	[47], 52
	Lamium purpureum	42
Peronospora linariae	Cymbalaria muralis	[49]
Peronospora lotorum	Lotus corniculatus	44, 49
	Lotus pedunculatus	35, 43, 44, 45, 46, 47, 52
Peronospora mayorii	Vicia cracca	49
Peronospora meconopsidis	Meconopsis betonicifolia	[47]
Peronospora meconopsidis	Papaver cambricum	41, 42, 43, 44, 46,
T Gronospora mocomopolais	T apavor cambridam	47, 48, 49, 50, 51
Doronosporo mocononcidio	Panayar aamnifarum	42, 43, 46, 49
Peronospora meconopsidis	Papaver somniferum	
Peronospora melandryi	Silene dioica	52
Peronospora meliloti	Melilotus altissimus	44
	Melilotus officinalis	44
Peronospora	Dorotheanthus bellidiformis	[35]
mesembryanthemi		
Peronospora minor	Atriplex patula	46, 48, 49, 52
·	Atriplex prostrata	46, 49, 50, 52
Peronospora myosotidis	Myosotis sylvatica	46, 49
Peronospora obovata	Spergula arvensis	46, 49
•	, ,	•
Peronospora oerteliana	Primula veris	[50]
	Primula vulgaris	35, 42, 44, [47], [48], 51
Peronospora ononidis	Ononis repens	46
Peronospora ornithopi	Ornithopus perpusillus	49
Peronospora parva	Stellaria alsine	49, 52
·	Stellaria graminea	49
	Stellaria pallida	46
Devenous varie	<u>-</u>	
Peronospora paula	Cerastium fontanum ssp.	35, 44,46
_	vulgare	
Peronospora phlogina	Phlox sp.	[46]
Peronospora pisi	Lathyrus oleraceus	[35], [41], [47]

Downy mildew/bilster-rustHostDistributionPeronospora polygoniPolygonum aviculare49, 52Peronospora potentillae-reptantisPotentilla reptans41, 49, 51Peronospora potentillae-sterilisPotentilla sterilis43, 44, 46Peronospora ranunculiRanunculus acris44, 46, 49, 52Ranunculus bulbosus35, 44, 46, 49Ranunculus flammula35, 43, 46, 47, 49Ranunculus repens35, 42, 43, 45, 4647, 48, 49, 50, 51, 52Peronospora romanicaMedicago lupulina41, 43, 44, 45, [47, 50, 50, 51, 52Peronospora rubiRubus fruticosus agg. Rubus fruticosus agg. × idaeus Rubus idaeus41, 42, 43, 49, 52Peronospora rumicisRumex acetosa ssp. acetosa43, 45, 46
reptantis Peronospora potentillae-sterilis Potentilla sterilis 43, 44, 46 Peronospora ranunculi Ranunculus acris 44, 46, 49, 52 Ranunculus bulbosus 35, 44, 46, 49 Ranunculus flammula 35, 42, 43, 45, 46 47, 48, 49, 50, 51, 52 Peronospora romanica Medicago lupulina 41, 43, 44, 45, [47, 50] Peronospora rubi Rubus fruticosus agg. 41, 42, 43, 49, 52 Rubus idaeus 51
Peronospora potentillae-sterilis Potentilla sterilis 43, 44, 46 Peronospora ranunculi Ranunculus acris 44, 46, 49, 52 Ranunculus bulbosus 35, 44, 46, 49 Ranunculus flammula 35, 43, 46, 47, 49 Ranunculus repens 35, 42, 43, 45, 46 47, 48, 49, 50, 51, 52 Peronospora romanica Medicago lupulina 41, 43, 44, 45, [47, 50] Peronospora rubi Rubus fruticosus agg. 41, 42, 43, 49, 52 Rubus idaeus 49 51
Peronospora ranunculi
Ranunculus bulbosus 35, 44, 46, 49 35, 43, 46, 47, 49 35, 42, 43, 45, 46 47, 48, 49, 50, 51, 52 Peronospora romanica Rubus fruticosus agg. 41, 43, 44, 45, [47, 50] Rubus idaeus 51 51 51 51 52 51 52 51 52 51 53 54 55 54 55 55 55 55
Ranunculus flammula 35, 43, 46, 47, 49 35, 42, 43, 45, 46 47, 48, 49, 50, 51, 52 Peronospora romanica Medicago lupulina 41, 43, 44, 45, [47
Ranunculus repens 35, 42, 43, 45, 46 47, 48, 49, 50, 51, 52 Peronospora romanica Medicago lupulina 41, 43, 44, 45, [47, 50 50 Peronospora rubi Rubus fruticosus agg. 41, 42, 43, 49, 52 Rubus idaeus 49 51
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A7, 48, 49, 50, 51, 52
Peronospora romanica Medicago lupulina 41, 43, 44, 45, [47] 50 Rubus fruticosus agg. Rubus fruticosus agg. × idaeus Rubus idaeus 51
Peronospora rubi Rubus fruticosus agg. Rubus fruticosus agg. × idaeus Rubus idaeus 50 41, 42, 43, 49, 52 49 51
Peronospora rubi Rubus fruticosus agg. Rubus fruticosus agg. × idaeus Rubus idaeus 51
Rubus fruticosus agg. × idaeus 49 Rubus idaeus 51
Rubus idaeus 51
Peronospora rumicis Rumey acetosa sen acetosa 43 45 46
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Peronospora schachtii Beta vulgaris ssp. maritima 49, 52
Beta vulgaris ssp. vulgaris [46]
Peronospora senneniana Lathyrus sylvestris 44
Peronospora sepium Vicia sepium 35, 42, 43, 44, 46
49, 50, 51
Peronospora sherardii Sherardia arvensis 46
Peronospora sordida Scrophularia auriculata 46
Scrophularia nodosa [43], 44, 46, [47],
[48], 49, 50, 51
52
Peronospora sp. Aquilegia vulgaris 41, 42, 44
Suaeda maritima 52
Peronospora sparsa Prunus laurocerasus 41
Rosa cv. 49
Peronospora stachydis Stachys arvensis 50
Peronospora symphyti Symphytum officinale 51
Peronospora tabacina Nicotiana cv. 45
Nicotiana sylvestris cv. 49
Nicotiana tabacum 49, 52
Peronospora tomentosa Cerastium glomeratum 35, 42, 43, 44, 46 47, 49, 52
Peronospora trifolii-arvensis Trifolium dubium 35, 42, 43, 44, 51
Peronospora trifolii-hybridi <u>Trifolium hybridum</u> [50]
Trifolium pratense 42, 46
Peronospora trifoliorum s.l. Trifolium medium 43, 51
Trifolium repens 43, 51
Trifolium sp. [47]
Peronospora valerianae Valeriana officinalis 49, 52

Downy mildew/bilster-rust	Host	Distribution	
Peronospora valerianellae	Valerianella carinata	46	
·	Valerianella locusta	46	
Peronospora verbenae	Verbena officinalis	44, 46	
Peronospora viciae	Vicia lathyroides	46	
·	Vicia sativa	44	
	Vicia sativa ssp. nigra	43, 45, 46, 49, 52	
	Vicia sativa ssp. segetalis	41, 42, 43, 44, 45,	
	, 3	46, 47, 49, 52	
Peronospora viciae s.l.	Lathyrus odoratus	[45], [46], [48]	
	Vicia orobus	43	
Peronospora violacea	Succisa pratensis	35, 42, 43, 45, 46, 48	
Peronospora violae	Viola arvensis	43, 44, 46, 50	
·	Viola riviniana	44	
	Viola sp.	[47]	
Plasmopara angelicae	Angelica sylvestris	41, 42, 43, 44, 45,	
		46, 48, 49, 50,	
		51, 52	
Plasmopara chaerophylli	Anthriscus sylvestris	35, 44, 46, 49, 50,	
	-	[51], 52	
Plasmopara densa	Odontites vernus	41, 43, 44, 46, [47],	
		49, 51, 52	
	Odontites vernus ssp.	44	
	serotinus		
	Rhinanthus minor	42, 43, 44, 46, [47],	
		48, 49, 50, 51, 52	
Plasmopara epilobii	Epilobium sp.	49	
Plasmopara euphrasiae	Euphrasia arctica ssp. borealis	44	
	Euphrasia confusa × nemorosa	44, 46	
	Euphrasia confusa ×	46	
	tetraquetra	4.0	
	Euphrasia nemorosa	46	
	Euphrasia officinalis agg.	35, 48	
	Euphrasia officinalis ssp. anglica	46	
	Euphrasia officinalis ssp.	44	
	pratensis	' '	
	Euphrasia sp.	48, 49	
Plasmopara nivea s.l.	Conopodium majus	42, 43, 44, 45, 46,	
		47, 48, 49, 50, 52	
	Ligusticum scoticum	46	
	Oenanthe crocata	35, 42, 43, 44, 46, 49	
	Smyrnium olusatrum	49, 52	
Plasmopara nivea s.s.	Aegopodium podagraria	35, 41, 42, 43, 44,	
,		45, 46, 47, 48,	
		49, 50, 52	

Downy mildew/bilster-rust	Host	Distribution
Plasmopara obducens	Impatiens walleriana	35, 46
Plasmopara pastinacae	Pastinaca sativa	[41]
Plasmopara pimpinellae	Pimpinella saxifraga ssp.	42, 46
	saxifraga	
Plasmopara pusilla s.s.	Geranium pratense	[43], 52
Plasmopara pusilla s.l.	Geranium pyrenaicum 51, 52	
	Geranium sylvaticum	[42]
Plasmopara saniculae	Sanicula europaea	[47]
Plasmopara viticola	Vitis vinifera	35
Plasmopara viticola	Vitis vinifera 'Purpurea'	47
Plasmoverna pygmaea	Anemone coronaria	[45], [46]
	Anemone nemorosa	35, 42, 43, 44, 45,
		46, 47, 48, 49,
		50, 51, 52
Pseudoperonospora humuli	Humulus lupulus	35, 42, 43, 44, 46
Pseudoperonospora urticae	Urtica dioica	35, 41, 46, [47], 51
Pustula obtusata s.l.	Jacobaea vulgaris	49
	Matricaria sp.	[47]
	Scorzonera humilis	41
	Senecio squalidus	44, 49, 52
Pustula obtusata s.l.	Senecio sylvaticus	46, 49, 52
	Senecio viscosus	43
	Senecio vulgaris	35, 41, 42, 43, 44,
		45, 46, 47, 48,
		49, 51, 52
Pustula obtusata s.s.	Tragopogon pratensis ssp.	35, 41, 43, 44, 45,
	minor	46, [47], 49, 52
Pustula spinulosa	Cirsium arvense	[47], 49, 50, 52
	Cirsium palustre	46, 49
	Cirsium vulgare	46, 49

The following table summarises the numbers of downy mildews and white blister-rusts so far recorded per Welsh vice-county in the column headed "DMs". Cardiganshire with 87 species of downy mildews and 147 host × downy mildew interactions (DM × Hosts) has been the most intensively studied of all the Welsh vice-counties. This total appears to be one of the largest published for any British vice-county. It has been particularly well-studied with respect to cultivated plants. If the 23 interactions that only occur on cultivated plants in Cardiganshire are subtracted from the total then the total number of native and naturalised vascular plants recorded on the BSBI data base in December 2019 for each of the Welsh vice-counties roughly correlates with the numbers of downy mildews so far recorded from the five vice-counties in bold type below that are considered by the authors to be the most intensively studied for these mildews. These same vice-counties all have significantly higher numbers of host species reported as supporting downy mildews.

Vice-county	DMs	DM × hosts	Total vascular plants*	Rusts	Smuts
35 Monmouthshire	40	51	1800	114	19
41 Glamorgan	32	39	2086	137	24
42 Breconshire	45	54	1568	131	24
43 Radnorshire	53	72	1302	112	34
44 Carmarthenshire	57	87	1682	164	29
45 Pembrokeshire	35	42	1433	107	14
46 Cardiganshire	87	146	1776	155	59
47 Montgomeryshire	43	51	1319	106	33
48 Merionethshire	27	31	1400	116	23
49 Caernarvonshire	74	119	1813	161	20
50 Denbighshire	35	39	1617	94	14
51 Flintshire	27	31	1554	69	5
52 Anglesey	52	71	1412	143	20

^{*} native and naturalised

Host plant status in the five best studied vice-counties:

Vice-county	Native	Archaeophyte	Neophyte/ naturalised	Casual/ cultivated
43	44	9	8	2
44	54	13	8	4
46	80	18	14	15
49	70	16	14	10
52	46	10	9	3

The figures above can be compared with the totals displayed in the table below for the vice-counties bordering Wales taken from the FRDBI and for Surrey and Cambridgeshire which have been subject to recent study.

Area of Search	DMs	Source
17 Surrey	106	B. Spooner pers. comm.
29 Cambridgeshire	78	C.D. Preston pers. comm.
34 W. Gloucestershire	50	FRDBI
36 Herefordshire	36	FRDBI
40 Shropshire	56	FRDBI
58 Cheshire	14	FRDBI

Glossary

The definitions provided here refer strictly to usage of the terms in this book.

antheridium (pl. antheridia) the male reproductive cell producing and containing gametes

aseptate lacking cross walls (septa), as in hyphae or sporangia

colony the mass of sporangiophores and sporangia, becoming visible

on the surface of the host

conidiophore modified hypha protruding from the host and producing

conidia

conidium (pl. conidia) asexual spores germinating by germ tubes (but not used for

downy mildews)

cuticle waxy layer covering the epidermis on the surface of the host

dichotomously branched of sporangiophores that branch repeatedly into two equal

halves (see "irregularly branched")

epidermis the outermost layer of cells on the organs of the host germ tube the germination hypha produced from a sporangium

haustorium (pl. haustoria) the absorption organ produced by a hypha within the cells of

the host

heterothallic when sexual reproduction requires, or benefits from, the

conjugation of separate individuals

hypha (pl. hyphae) the filament of the mildew

irregularly branched of sporangiophores that branch repeatedly into unequal

halves (see "dichotomously branched")

mycelium a mass of hyphae

oogonium (pl. oogonia) the female reproductive cell producing female gametes and

producing oospores on fertilisation

oospore thick-walled resting spore produced by fertilisation within an

oogonium

pyriform pear-shaped

septate with cross-walls, as in hyphae or sporangia

septum (pl. septa) internal cross walls dividing a hypha or sporangium into cells sorus (pl. sori) the distinct mass of sporangiophores and sporangia in the

blister of a white blister-rust

sporangium (pl. sporangia) asexual spores produced from the sporangiophores, and

producing either germ tubes or zoospores

sporangiophore modified hypha protruding from the host and producing

sporangia

stomata small pores in the host surface tissues allowing passage of

gases

trichotomously branched of sporangiophores that branch into three equal parts

vesicular bladder-shaped

zoospore motile spore produced from a sporangium

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Searching for Downy Mildews



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It is frequently remarked by field mycologists that downy mildews can take some finding! The authors of this publication would concur with this statement. Fewer than a score of species have been reported with any degree of regularity in Wales. They are mostly found on annual and herbaceous perennial plants. If time is limited the most profitable sites to search tend to support large numbers of annual plant species such as the disused sand quarry near Cardigan illustrated above, brown-field sites (see below right) and gardens (see below left). The road verge adjacent to a high-quality nature reserve has often produced more records than the reserve! But wherever you are they are worth searching for.



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