Life Cycles of the Rusts

(Pucciniales, syn. Uredinales; Basidiomycota)

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1. **INTRODUCTION**: **the names of spore stages; and dikaryons and monokaryons.**

Getting to grips with Rust life cycles can be difficult. In an attempt to help, we have written descriptions of the various kinds of life cycles that may be encountered while recording in the field. These are often complex and the terminology used to describe them in books and papers is sometimes confusing, but we have done our best to be straightforward and unambiguous.

1.1 What's in a name?
One especially confusing matter is that the scientific names used by plant pathologists to describe the Rusts, and the various kinds of spores they produce, have changed over the years. These changes, although in most cases only small, are nevertheless sufficient to cause uncertainty when the words in question are used in print.

The most recent change has been the name for the Rust fungi as a group. For years this was the order **Uromyces** (within the group Basidiomycota in the kingdom Fungi). The scientific word Uromyces is based on the Latin/Greek *urere*, to burn or singe, a reference to the orange/yellow or flame colour of the lesions formed on host leaves or stems infected by Rusts (Figure 1).

Figure 1. A flame-coloured lesion of *Phragmidium rosae-pimpinellifoliae* on a stem of *Rosa pimpinellifolia*. Rosemary Winnall

Recently, however, Uromyces has been changed to **Pucciniales**, a name representing the largest genus of Rust fungi within the order: the genus *Puccinia*, which accounts for more than half of the c.7000 species of Rusts worldwide. This genus was originally named by the early Italian plant scientist Pier'Antonio Micheli (1679-1737), in honour of his near-contemporary, Tommaso Puccini (1666-1726), Professor of Anatomy in Florence. The change to Pucciniales represents a switch from a name based on a description of one aspect of Rusts in general - spore colour - to the name of the genus most representative of the order as a whole.

Most of the name changes relating to individual spore stages in Rust life-cycles, however, have resulted from discussions about the correct way to construct the technical names from the original ancient Latin or Greek words used as a basis for the names. A good example is the spelling of the word *urediniospore*, the name now given to the asexual spore whose function in most Rust life-cycles is to disperse the infection widely and rapidly to other plants of the same host species during the summer months. We have already noted above that the first half of this name is descriptive, being based on the colour of these spore masses. The second half, spore, is derived from the Greek *sporos*, seed, this being a nod to the fact that *urediniospores* have a function similar to that of seeds, even though their structure is much simpler than that of a higher plant seed.

The spelling of this spore name when David Ingram was an undergraduate in the early 1960s was *uredospore*. Later it changed to *urediospore* and a little later still was changed again to *urediniospore*. All these spellings may be seen in books and papers, so we shall use here the most recent spelling, with the earlier synonyms in brackets, thus: urediniospore (syn. uredospore, urediospore). We shall follow the same convention with the names of other spore stages and technical words as we describe the various life cycles of Rusts below.

1.2 Dikaryons and monokaryons
Before getting to grips with the life cycles themselves, it is also necessary to know what **dikaryons** and **monkaryons** are (Greek *di* and *monos*, two and alone, respectively + *karyo*, a nut or kernel).

The cells of Rusts are, for a significant part of their life cycles, **dikaryons**. This means that each cell of their **hyphae** - the tube-like structures that make up their 'bodies' - contains **two haploid nuclei**, each having only a single set of the chromosomes that carry the genetic information. Since each nucleus in a di-

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karyotic Rust cell, as we shall show, is derived from a different parent, the cell is *functionally* **diploid** (the state of the *single* nucleus in a body cell of a higher plant or animal, which contains two sets of chromosomes, one from each parent).

During the life cycle of a Rust fungus, there are two stages when some or most of the cells become **monokaryotic**, a state in which each cell has only a **single, haploid nucleus**. These stages are concerned with genetic mixing. Thus, at one stage, fusion of two monokaryotic **cells** from different parents creates new dikaryons. At another stage, fusion of the two haploid **nuclei** within some dikaryotic cells, followed by a period of diploidy and then meiosis (a reduction division with genetic mixing) creates new monokaryons.

To achieve such nuclear acrobatics, several different spore stages may be involved, sometimes distributed between two different host plants. To see how this works in practice, it is necessary to examine in detail the most complex type of Rust life-cycle, which includes two hosts and many spore stages.

Searching for Rusts, Button Oak Meadow Rosemary Winnall

2. DETAILED LIFE CYCLES OF RUSTS WITH TWO HOSTS AND MANY SPORE STAGES (DIOECIOUS & MACROCYCLIC)

2.1 *Melampsora rostrupii* (syn. *M. populnea*[1]), whose hosts are *Mercurialis perennis* (Dog's Mercury) and *Populus* spp. (Poplars and close relatives).

In Rusts with two hosts, the complicated life cycle is neatly integrated with the complementary life cycles of the two alternate hosts, thereby allowing reproduction and dissemination of the pathogen to take place throughout the spring and summer months.

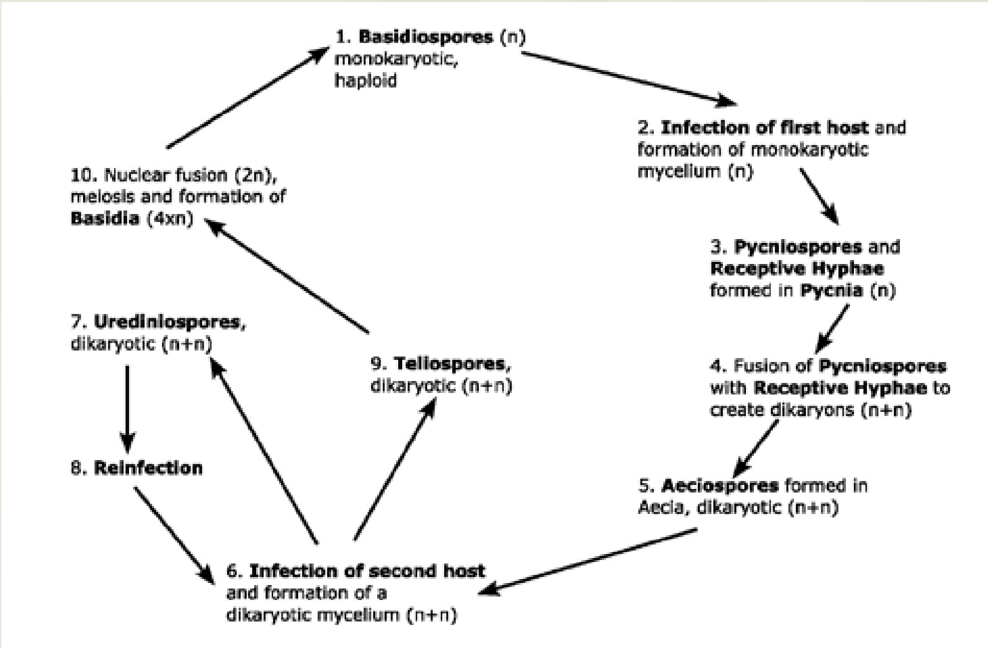
Melampsora rostrupii is a good species to begin with, for various reasons:

- it is widespread, easy to find in Spring and is known to occur in the Wyre area;
- it is a **macrocyclic** (syn. long life-cycle) Rust in which all possible spore stages occur in its life cycle;
- it is a **dioecious** Rust (from the Greek *di*, two + *oikos*, loosely, a family home), meaning that the various spore stages of the life cycle are distributed between two **alternate hosts** which become infected in sequence, firstly Dog's Mercury (*Mercurialis perennis*) and then later in the season, Aspen (*Populus tremula*) or the closely related White Poplar (*Populus alba*).

2.2 Where to begin?

This is a major difficulty when writing about specific Rust life-cycles such as that of *M. rostrupii*, for being 'cycles' they are, by definition, circular or continuous processes. For consistency, however, we shall always begin Rust life cycles in the Spring, with infection of the first (spring) host by **basidiospores** (from the Greek, *baseidion*, small base + *sporos*, seed), as in Figure 2.

[1] *Melampsora populnea* is an aggregate name used to embrace all Rusts that are physically identical to *M. rostrupii*, but genetically different in that they have alternate hosts other than *Populus tremula* and ***P. alba***.



Key:
1-5 = stages on the first (spring) alternate host;
6-9 = stages on the second (summer and autumn) alternate host;
10 = winter-spring stages of dormancy and germination;
n = monokaryotic/haploid;
n + *n* = dikaryotic/effectively diploid;
2n = diploid (top left of cycle, between nuclear fusion & meiosis);
4 x *n* = four haploid nuclei (top left, after meiosis & before formation of basidia).

Figure 2. The spore stages of a long life-cycle, dioecious Rust such as *Melampsora rostrupii*. Drawing by G. Hill

2. 3 STAGES 1-5: First Alternate Host, Dog's Mercury (*Mercurialis perennis*)

2.3.1 First Phase: basidiospores, infection, pycnia, pycniospores and receptive hyphae (stages 1-4)

When the leaves of Dog's Mercury appear in early spring there is no sign of disease. Very soon, however, some plants may become infected by haploid **basidiospores** of *Melampsora rostrupii*. These are produced as the final spore stage at the end of the previous year's life-cycle and their origin will become clear as the new cycle reaches its climax (see below). In moist conditions, most viable basidiospores landing on a Dog's Mercury leaf create an **infection focus** where monokaryotic hyphae develop in the tissues and very soon produce minute, spot-like, honey coloured **pycnia** (from the Greek *pyknos*, close packed; syn. spermagonia).

If, at this stage, the upper surfaces of the spots are examined with a hand lens, it will be found that the pycnia are in fact tiny lens-shaped structures embedded in the leaf surface, just below the epidermis. When the weather is damp, these pycnia ooze droplets of slime and if these are examined with a microscope, they are found to be full of minute, non-motile spores called **pycniospores** (syn. spermatia). In addition, also seen to be emerging from the mouths of the pycnia, will be simple hyphae called **receptive hyphae**. Both the pycniospores and receptive hyphae are uninucleate and haploid (thus **monokaryotic**).

The slime with its load of pycniospores may be carried from one infected host to another by insects during foraging. If a pycniospore from one host becomes deposited on a receptive hypha on a different host, it sticks to it and the two then fuse to create a cell with two haploid nuclei (a **dikaryon**). This process is similar in many ways to cross fertilization in the reproduction of plants and animals, but differs in that the two nuclei do not fuse, but

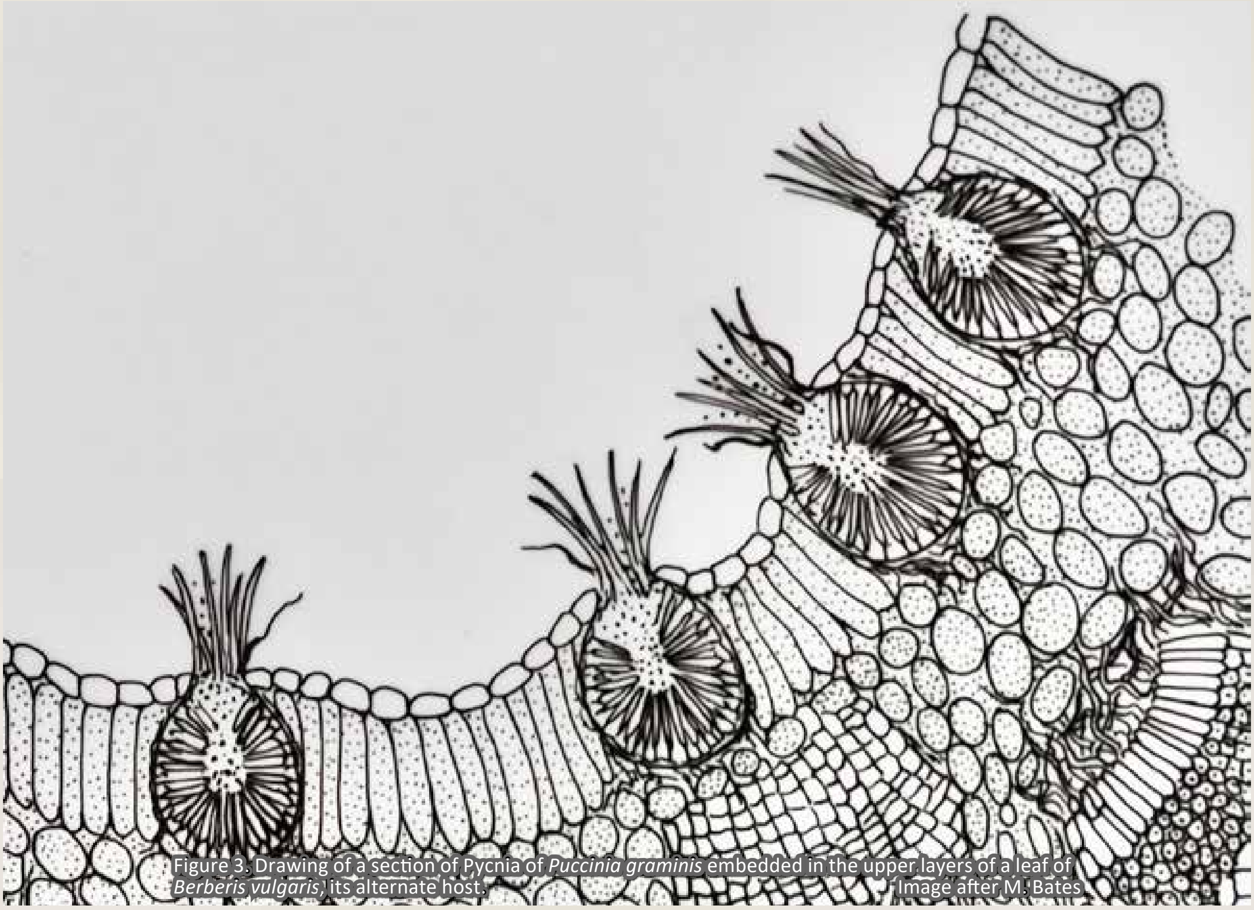


Figure 3. Drawing of a section of Pycnia of *Puccinia graminis* embedded in the upper layers of a leaf of *Berberis vulgaris*, its alternate host. Image after M. Bates

remain as separate entities within the dikaryotic cell. The cell thus carries complementary, haploid nuclei and is genetically equivalent to a cell with a single diploid nucleus.

Note that although the pycnia of *Melampsora rostrupii* are lens shaped, in other Rust species they are often flask-shaped, as in *Puccinia graminis*, cause of Black Stem Rust of grass hosts, on its alternate host *Berberis vulgaris* (Barberry).

***2.3.2 Second Phase: Aecia and aeciospores* (stage 5)**

Following fusion of the pycniospores and receptive hyphae, dikaryotic hyphae begin to form and grow within the leaf tissue of Dog's Mercury. This may occur either by: repeated division of the fused (and therefore dikaryotic) cell; or by repeated division of the introduced nucleus and migration of the daughter nuclei to adjacent monokaryotic cells.
Eventually, groups of dikaryotic hyphae begin to aggregate near the lower, inner surface of the Dog's Mercury leaf, below the groups of pycnia from which they originated, to form much larger, deeper orange coloured, non-motile spore-producing structures called **aecia** (from Greek *aikia*, injury; syn. aecidia). When mature, the aecia break through the epidermis, are powdery in appearance and are packed with bright orange, dikaryotic spores called **aeciospores** (syn. aecidiospores). If examined with a microscope these will be found to be globoid to angular in shape, with a thick, densely warty wall (Figures 4a - c).

Note that although the aecia of *Melampsora rostrupii* are often relatively amorphous, as in the photographs, in many other Rust species they are clearly cup shaped, as with *Puccinia graminis*, cause of Black Stem Rust of grasses, on its alternate host, Barberry (Figure 5).

a

b

c

Figure 4, a-c. Pycnia and Aecia of *Melampsora rostrupii* on leaves and a stem of its alternate host, Dog's Mercury (*Mercurialis perennis*): a. infected leaves and stems on a whole plant; b. a lower leaf surface with minute Pycnia appearing faintly in the centre of a ring of large Aecia; c. enlarged view of roughly cup-shaped, ragged-edged Aecia. Image 'a' by J. Ingram; images 'b' and 'c' by R. Winnall.

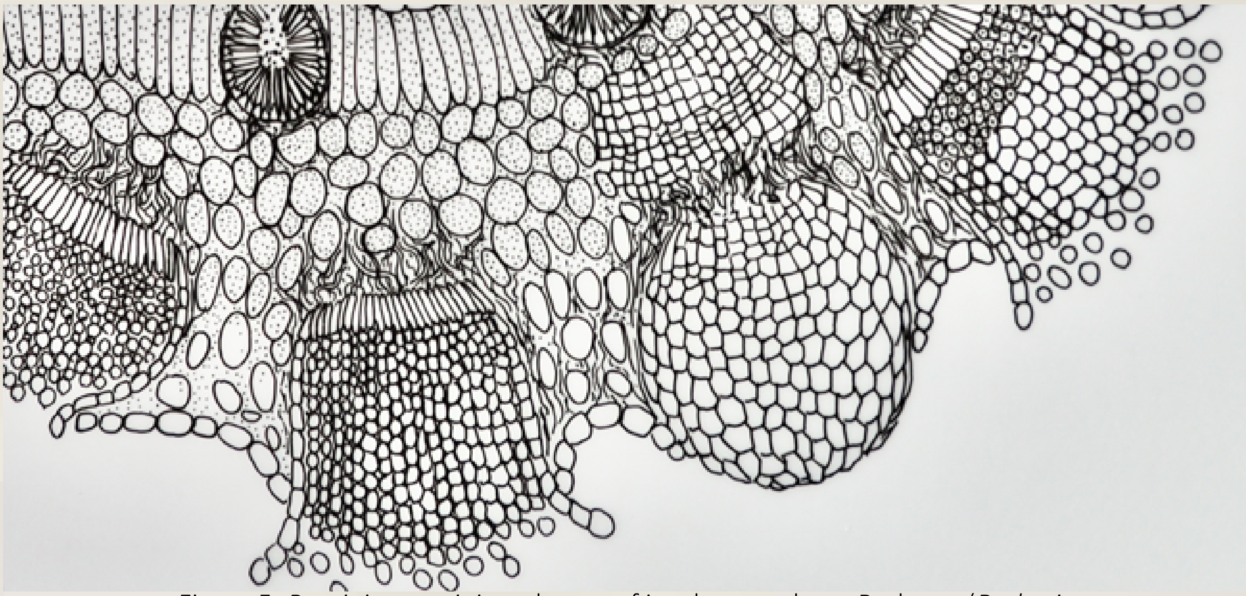


Figure 5. *Puccinia graminis* on leaves of its alternate host, Barberry (*Berberis vulgaris*): drawing of sections showing clearly cup-shaped Aecia (one yet to open) with chains of Aeciospores. Image after M. Bates.

2.3.3 STAGES 6-9: Second Alternate Host, Aspen (Populus tremula) or White Poplar (P. alba)

First Phase: infection, uredinia and urediniospores. The aeciospores mature on the Dog's Mercury leaves at about the same time as the young leaves of the **alternate host**, Aspen or White Poplar, are beginning to grow. The aeciospores are carried to these by the wind, and if sufficient moisture is available, they germinate to form a germ tube which infects the leaf via a stoma and establishes an intercellular, dikaryotic mycelium.

Eventually, hyphae aggregate at scattered points under the lower epidermis of the Aspen or White Poplar and form yellowish-orange lesions called **uredinia** (Figure 6; from Greek *urere*, to burn). In these, elliptical, spiny-walled, single-celled, non-motile, dikaryotic **urediniospores** are produced (syn. uredospores, urediospores). These are released into the air to disperse the pathogen to uninfected leaves on the same tree, or to new Aspen or White Poplar trees in the surrounding area. This process continues throughout the summer, with each new infection producing more urediniospores which in turn infect further leaves or trees, and so on. Thus, the population of infected leaves on the host trees in the community of *Populus* species increases exponentially.

Note: The urediniospores of *Melampsora rostrupii* are ovoid and spiny. The urediniospores of most Rust fungi are globose to ovoid, and have relatively thin walls that may be smooth, spiny or warty, depending on the species. Most also have two or more pores around the equator, the number being characteristic for each species.

Figure 6. Urediniospore lesions of *Melampsora rostrupii* on leaves of Aspen: left, upper leaf surface; right, lower surface. C. Taylor.

Second Phase: telia and teliospores. Later in the summer the dikaryotic hyphae begin to form dark brown ***telia*** (from Greek *telos*, end, ultimate object or aim). These occur immediately below the epidermis and are distributed all over the leaf surface. In them, brown, single-celled, thick-walled, elongate and round-ended resting spores, the **teliospores** (syn. teleutospores) form. Each teliospore is a dikaryon, but before **winter dormancy** sets in, the two nuclei fuse to create one **diploid nucleus** that contains the DNA from both parents.

Note The teliospores of Rust fungi vary enormously in shape and cell number according to the genus: for example, in some, such as Melamposora and Uromyces, they are rounded and single-celled; in *Puccinia* and *Gymnosporangium* they are two-celled, often with an equatorial waist (Figure 7); while in others, such as *Phragmidium*, they are elongate and multicellular.

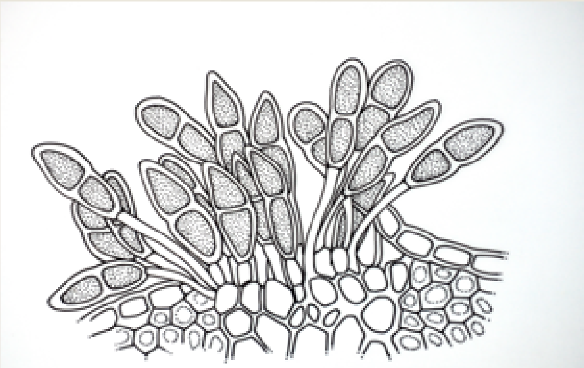


Figure 7. Drawing of teliospores of *Puccinia graminis*. Image after M. Bates.

2.3.4. STAGE 10: winter-spring stages of dormancy and germination of the teliospores to produce basidia and basidiospores

The **teliospores** of *Melampsora rostrupii* probably overwinter on dead Aspen or White Poplar leaves. During the following spring they emerge from their dormancy and the diploid nucleus in each one undergoes a meiotic division to form four haploid nuclei. In each of these nuclei the DNA from the original two parents is mixed by the crossing over of chromosomes and related processes during the division process.

During nuclear division or immediately after it, a short hypha, the **basidium** (Greek *boseidion*, small base) grows out from each cell of the teliospore and buds off four **basidiospores**, each containing one of the four haploid nuclei resulting from meiosis (thus each spore is a monokaryon). The basidiospores are then carried on air currents to **the first host again (Dog's Mercury)**, which they **infect, beginning the cycle once more.**

3. OTHER DIOECIOUS, MACROCYCLIC RUSTS
Many other dioecious, macrocyclic Rusts exist, including those listed below.

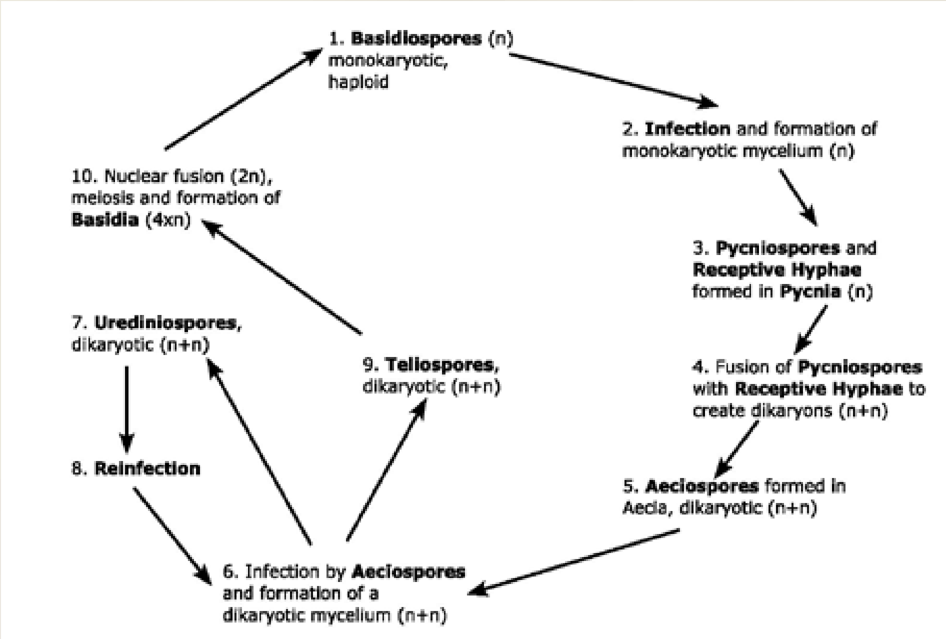
Gymnosporangium cornutum (Juniper Rust; alternate hosts *Sorbus aucuparia* and *Juniperus communis*);
Puccinia graminis (Black Stem Rust; alternate hosts *Berberis vulgaris* and many grasses, including the cereals wheat, barley and oats);
Puccinia poarum (Meadow Grass Rust; alternate hosts *Poa* species and *Tussilago farfara);*
*Puccinia sessilis (*Reed Canary Grass Rust; alternate hosts *Allium ursinum* and *Phalaris arundinacea);*
Uromyces dactylidis (Cock's-foot Rust; alternate hosts, *Dactylis* spp. and *Ficaria verna*).

In each of these Rusts, as with *Melampsora rostrupii*, the complicated life cycle is neatly integrated with the life cycles of its two alternate hosts, thereby allowing reproduction and dissemination of the pathogen to take place throughout the spring and summer months. Moreover, the teliospore stage enables Rusts to survive any inclement period, according to species, whether it be frost, drought or high temperature, when neither host may be able to grow normally. Finally, phases that lead to the mixing of genetic information are built into the life cycles and ensure that the basidiospores arising from the teliospores are furnished with new combinations of genetic information to increase the likelihood of at least some members of the population being able to adapt to any changed environmental conditions that may have arisen during the period of dormancy.

4. LIFE CYCLES OF THE RUST FUNGI WITH ONLY ONE HOST (AUTOECIOUS AND MACROCYCLIC OR MICROCYCLIC)

4.1 Introduction
The scientific word used to describe Rusts having only one host is **autoecious**, from the Greek *autos* = self + *oikos* = a family home. Under this overall heading, we shall describe the two principal groups, as follows:

- macrocyclic (long life-cycle) and autoecious: Rusts with a life cycle in which all the spore stages are represented (Figure 8);



Key:
1-5 = spring stages;
6-9 = summer and autumn stages;
10 = winter dormancy and germination.
n = monokaryotic/haploid;
n + *n* = dikaryotic/effectively diploid;
2*n* = diploid (top left of cycle, between nuclear fusion & meiosis);
4 x *n* = four haploid nuclei (top left, after meiosis & before formation of basidia).

Figure 8. Spore stages of the autoecious, macrocyclic Rust, *Puccinia violae*.
Drawing by G. Hill

- microcyclic (short life-cycle) and autoecious, Rusts with a life cycle in which some spore stages are omitted.

4.2 Rusts with life cycles restricted to a single host, on which all the spore stages are represented (autoecious and macrocyclic): **e.g. Violet Rust (*Puccinia violae*)**

We are beginning with Violet Rust since it is a common and typical autoecious, long life-cycle Rust that occurs in Wyre. *Puccinia violae* may infect a wide range of *Viola* species, including *V. canina*, *V. hirta*, *V. odorata*, *V. richenbachiana*, *V. riviniana*, *V. tricolor* and various *Viola* cultivars.

***4.2.2 First Phase: basidiospores, infection, pycnia, pycniospores and receptive hyphae, aecia and aeciospores* (Stages 1-5 in Figure 8)**

In spring, the susceptible *Viola* species appear healthy. Soon, however, some plants may become infected, **presumably** by haploid **basidiospores** produced by teliospores that were the final spore stage at the end of the previous year's life cycle (their origin will become obvious as the new cycle reaches its climax, below).

Note: we have used the word '**presumably**' in the above paragraph because published evidence to support the supposition is not available. It will be necessary for us to use this word and the word '**probably**' in the accounts that follow, for similar reasons.

In moist conditions, each viable basidiospore landing on a susceptible Violet leaf creates an **infection focus** where **monokaryotic hyphae** develop in the living tissues. Very soon, yellowish **pycnia** form just below both surfaces of the leaves. These will be seen to be flask shaped if examined with a hand lens. They produce droplets of sweet fluid that is attractive to insects and is loaded with minute **pycniospores**. In addition, also seen to be emerging from the mouths of the pycnia, will be simple hyphae called **receptive hyphae**. Both the pycniospores and receptive hyphae are uninucleate and haploid (thus **monokaryotic**).

If the sweet fluid with its load of pycniospores is carried by insects from one infected leaf to another, either on the same plant or on a different plant, and if a pycniospore from the first leaf becomes deposited on a receptive hypha on a different leaf, it will stick to it and the two will then fuse to create a cell with two haploid nuclei (thus it is **dikaryotic**). This process is similar to cross fertilization in the reproduction of plants and animals, but differs in that the two nuclei do not fuse, but remain as separate entities within the dikaryotic cell. The cell thus carries complementary, haploid nuclei and is **genetically equivalent to a cell with a single diploid nucleus**.

A **dikaryotic mycelium** next develops from this cell and grows between the cells of the living leaf tissues. Eventually, the hyphae begin to aggregate and prominent orange **aecia** form in groups, mainly on the lower surfaces of the leaves, but also on other infected structures such as stems and petioles. The **aecia** are clearly cup-shaped (Figure 9), with a torn, white margin and the infected host tissues frequently exhibit swelling or distortion, including bending, suggesting hormonal disturbance. The orange **aeciospores**, formed within the aecia, are globoid to ellipsoid and minutely **verrucose** (covered with wart-like surface structures; Latin, *verruca*, a wart).

4.2.3 Second Phase: re-infection, uredinia, urediniospores, telia, teliospores, basidia and basidiospores **(Stages 6-9 in Figure. 8)**

Following **re-infection of the same host species** by the **aeciospores**, **uredinia** (syn. uredia, urediosori) begin to form, scattered or in groups, on both leaf surfaces. The powdery **urediniospores** formed in the uredinia are cinnamon brown in colour, globoid to ellipsoid, and **echinulate** (spiny; Greek *ekhinos*, hedgehog, sea urchin).

The **telia** (syn. teleutorsori) form next, on the lower surfaces of leaves, often on yellowish spots. These are small, powdery and chocolate brown in colour. The reddish brown **teliospores** (syn. teleutospores) formed in them are ellipsoid to oblong in shape, two-celled (the upper one larger than the lower and somewhat flattened at the apex), and are **minutely verruculose** (covered with very small surface wart-like structures).

Each teliospore cell is a dikaryon, but before a period of **dormancy** sets in, the two nuclei probably fuse to create one **diploid nucleus** per spore that contains the DNA from both parents.

Figure 9. Developing cup-shaped aecia of Violet Rust (*Puccinia violae*) on a lower leaf surface of Common Dog-Violet (*Viola riviniana*). R. Winnall.

***4.2.4 Third Phase: winter dormancy and germination to produce basidia and basidiospores* (Stage 10 in Figure. 8)**

The teliospores probably overwinter in a state of dormancy on dead host leaves or other debris, or in the soil. **During the following spring the teliospores emerge from their dormancy** and the diploid nucleus in each one undergoes a meiotic division to form four haploid nuclei. In each of these nuclei the DNA from the original two parents is mixed by the crossing over of chromosomes and related processes during the division sequence.

During nuclear division or immediately after it, a short hypha, the **basidium,** grows out from each cell of the teliospore and buds off four **basidiospores**, each containing one of the four haploid nuclei resulting from meiosis (thus each spore is a **monokaryon**). The basidiospores are then carried on air currents to newly emerging *Viola* plants where they initiate a new infection.


Figure 10. *Triphragmidium ulmariae* (Meadowsweet Rust) on *Filipendula ulmaria.* R. Winnall.

4.3 Other common examples of autoecious, macrocyclic Rusts

Triphragmidium ulmariae (Meadowsweet Rust, host *Filipendula ulmaria) (Figure 10)*;

Phragmidium mucronatum (Rose Rust, hosts *Rosa* spp. and cultivars);

Phragmidium fragariae (Barren Strawberry Rust, host *Potentilla sterilis*);

Puccinia punctiformis (Creeping Thistle Rust, host *Cirsium arvense*).

Puccinia punctiformis is unusual in that it not only produces pycniospores, aeciospores, urediniospores and teliospores, **but is also able to overwinter as a systemic mycelium that permeates the underground rhizomes of its perennial host**. When, in spring, new shoots emerge from the infected rhizomes, the mycelium permeates these too and produces **pycnia** with **pycniospores** all over the stems and leaves, leading to formation of **aecia** and **aeciospores**. The infected plants are tallish and paler in colour than normal, the result of hormonal disturbance, and have a sweet, honey-like odour. This, presumably, attracts insects, which transfer the pycniospores to uninfected plants. Other uninfected plants may become infected by **urediniospores** carried by wind from spring-infected plants during the summer. **Teliospores** are produced in late summer and the **basidiospores** formed by these immediately infect buds on stems and rhizomes, leading to the systemically infected rhizomes that will overwinter.

Puccinia menthae (probably an aggregate species since its hosts include many *Mentha*, *Oreganum* and *Clinopodium* species and cultivars). This Rust is also unusual in that **pycniospores and aeciospores form on emerging shoots** during very early spring, giving the impression that these may have been produced by a systemic mycelium that had overwintered in the stolons, as with *Puccinia punctiformis*. However, there is little evidence of overwintering in this way, and the spore stages formed on the emerging shoots probably result from early infections by **basidiospores produced from overwintered teliospores** on debris or the surface of underground parts of the plants. Thereafter, **aeciospores** infect the same or uninfected shoots, which then produce **urediniospores**, which infect further plants, and **teliospores**, which overwinter.

4.4 Rusts with life cycles restricted to a single host, on which a reduced number of spore stages is formed (autoecious and microcyclic)

Where a Rust host has only a short period of vegetative growth, as with many spring-flowering species or species that grow on the tops of mountains or at high latitudes, a shortened life cycle may ensure a rapid throughput of the fungus before the end of the growing season. We shall describe two common examples.

4.4.1 Lesser Celandine Rust, Uromyces ficariae (host Ficaria verna; syn. Ranunculus ficaria)

This is a common, easy to spot **autoecious**, **microcyclic** native Rust that infects one of the earliest and most short-lived wild flowering plants of spring. The only spores produced are **teliospores** and **basidiospores**. It is presumed (but has not been demonstrated experimentally) that the dikaryotic **teliospores**, having undergone nuclear fusion to become **monokaryotic** and **diploid**, survive from one year to the next either on the surface of the underground tubers of the host, in host debris or in the soil.

Early the following spring, these previous year's **teliospores** germinate. It is again presumed that first the diploid nucleus undergoes meiosis to form four haploid nuclei and these then migrate, via the basidia, into the four developing **basidiospores**. These infect the young host plants and form a largely **monokaryotic**, **haploid** mycelium in the living tissues. The mycelium then becomes **dikaryotic**, presumably as a result of nuclear migration, just before the dark brown **telia** are formed. These occur in orbicular or elongate clusters on yellowish spots on petioles and both surfaces of leaves (Figure 11).

Finally, the telia produce dark brown to almost black, single celled, thick walled **teliospores**. These are ovoid, with a conical papilla at the apex, giving them the overall form of a lemon. It is presumed that following nuclear fusion to become **diploid**, the teliospores then enter a dormant period, before beginning the short life cycle again the following spring.

4.4.2 Bluebell Rust, Uromyces muscari (hosts: Hyacinthoides non-scripta, H. hispanica and some Muscari and Scilla species and cultivars).

This is another very common **autoecious**, **microcyclic** Rust, which produces only **teliospores**. These are **dikaryotic,** and having undergone nuclear fusion to become **monokaryotic** and **diploid**, survive from one year to the next either on the surface of the underground parts of the plants (mainly outer bud scales and old flower stem bases), or in the soil.

In spring, following **basidiospore formation**, as in *Uromyces ficariae*, and infection of emerging leaves, pallid to yellowish, round to elongate or lens shaped **telia** form (Figure 12). These are at first covered by the epidermis, which eventually splits to reveal the dark brown **teliospores**, often in concentric rings (Figure 13). The individual teliospores are brownish, single celled, thick-walled and roundish to ellipsoid in shape, sometimes marked with faint ridges. As the infected leaves senesce (die down), **green islands** of chlorophyll retention may be seen around the lesions, suggesting hormonal disturbance (Figure 13).

Figure 11. Telia of *Uromyces ficariae* on Lesser Celandine (*Ficaria verna*). J. Young.

Finally, the teliospores enter a phase of dormancy, their numbers being swelled by additional telia which continue to form on underground leaf and flower stem bases after those above the surface have died down. They then survive until the next year, when they begin the cycle again.

Figure 12. Telia of Bluebell Rust, *Uromyces muscari*. R. Winnall.

Figure 13. Telia with dark brown teliospores of *Uromyces muscari* on a senescing leaf of a *Hyacinthoides* species showing green islands. D. S. Ingram

4.5 Appendix: Introduced (non-native) autoecious, microcyclic Rusts

The two we shall describe are frequently seen on cultivated garden plants.

4.5.1 Mallow and Hollyhock Rust, Puccinea malvacearum (hosts: members of the family Malvaceae)

This is a common, **introduced autoecious**, **microcyclic** Rust that may be seen throughout spring, summer and autumn. It is especially noticeable in gardens on Hollyhocks and produces only **telia** and **teliospores** (Figure 14).

Puccinia malvacearum was originally introduced from Chile, where it is believed to be native. It was first described in about 1852 and subsequently appeared in Australia, Spain, France, England and eventually, from 1874 to 1890, in most other European countries. It was also found in South Africa in 1875, North America in 1886 and is now almost ubiquitous. It may therefore be regarded as an alien across much of the world.

The **telia** appear as yellowish to rusty-orange, round to elongate spots, closely scattered across the upper surfaces of leaves, and on petioles and stems. On the undersides of

Figure 14. Telia and teliospores of *Puccinea malvacearum* on the undersides of basal leaves of Musk-mallow (*Malva moschata*). Rosemary Winnall.

Figure 15. Uredinia with urediniospores of *Puccinia antirrhini* on a rather scruffy overwintered garden *Antirrhinum*. D. S. Ingram

leaves and on stems these spots are usually raised and reddish to dark-brown in colour. The **teliospores** are two-celled, with a waist where the cells join. **They germinate where they are produced** and after nuclear fusion and meiosis, four uninucleate, haploid basidiospores form **and infect emerging leaves on the same or other plants.**

The pathogen **overwinters as teliospores in telia on lower leaves, where these persist, and especially on stem bases**. These then re-infect new leaves of the same host where they re-establish the binucleate (dikaryotic) mycelium, probably by exchange of nuclei between mycelia.

4.5.2 Snapdragon (Antirrhinum) Rust, Puccinia antirrhini (hosts, cultivated Antirrhinum majus and A. glutinosum)

This is a common, **non-native autoecious, short cycle** Rust that is a pathogen of cultivated *Antirrhinum* species and cultivars in gardens, and on feral *Antirrhinum* plants. It originated in western North America and was introduced to Europe in the last century. It does not produce pycniospores or aeciospores, but **does produce uredinia** and **dikaryotic urediniospores** in large numbers, mainly on leaves (Figure 15), and rarely, **teliospores**, in very small numbers, also on leaves.

It is presumed that in the UK it cycles continually by means of infection and reinfection of plants by **urediniospores** and normally overwinters in this form, either on glasshouse-grown plants, or on the occasional host plant that survive the winter in neglected garden areas, as in Figure 15.

5. Sources of Information About the Identification and Biology of the British Native Rust Fungi

Ellis, M. and Ellis, J. (2017). *Microfungi on Land Plants: An Identification Handbook, 2nd edn*. (This is often useful as a starting point when trying to identify a Rust specimen, but is now rather dated and is not comprehensive.)

Henderson, D.M. (2004). *The Rust Fungi of the British Isles – a Guide to Identification by Their Plant Hosts*, The British Mycological Society, now downloadable from: www.aber.ac.uk/waxcap/links/. (An easy to use and valuable guide to British Rust fungus identification; see also, Wilson and Henderson [1996]; Woods et al [2015] recommend that it be used in conjunction with Malcolm Storey's excellent images at: www.bioimages.org.uk.)

Ingram, D.S. and Robertson, N.F. (1999). *Plant Disease: A Natural History* (Chapter 12, pp. 176-200). Harper Collins, London. (A useful introduction to native British Rusts.)

Klenke, F. and Scholler, M. (2015). *Pflanzenparasitische Kleinpilze*, Springer Spectrum, Berlin. (This German language monograph has been recommended to DSI as being valuable for information on the biology and identification of most of the native British Rust fungi. It may be purchased as an electronic version [and perhaps run through a translation programme].)

Littlefield, L.L. (1981). *Biology of the Plant Rusts – An Introduction*. Iowa State University Press, Ames, Iowa. (A fascinating book, mainly about the biology of Rusts of cultivated plants, although now somewhat out of date)

Plant Parasites of Europe. Website, https://bladmineerders.nl (a most valuable resource).

Termorshuizen, A. and Swertz, C.A. (2011). *Roesten van Nederland*. Termorshuizen. (This up-to-date guide that includes most British Rusts is available as a hard copy book or to download, and has descriptions in English as well as Dutch.

Tronsmo, A.M., Collinge, D.B., Djurle, A., Munk, L., Yuen, J. & Tronsmo, A. (2020). *Plant Pathology and Plant Diseases*, CABI, Wallingford. (An up-to-date general plant pathology text book. The pathogens dealt with are mainly the cause of disease on crop plants, but species on native plants are often referred to. For anyone interested in gaining an overview of professional European and UK Plant Pathology, it is a valuable resource.)

Wilson, M. and Henderson, D. M. (1996). *British Rust Fungi.* Cambridge University Press, Cambridge. (The most comprehensive monograph on the taxonomy and biology of British Rusts. Now out of print, but second-hand and reprint copies of this old and invaluable resource are still available. A drawback to be aware of is that although the book includes drawings of many spore stages, the identification key is based on the description of one spore stage only, the teliospore, which is frequently not present on diseased plants.)

Woods, R.G., Stringer, R.N., Evans, D.A. and Chater, A.O. (2015). *Rust Fungus Red Data List and Census Catalogue for Wales*. A.O. Chater, Aberystwyth. (A most valuable introduction to the biology of native British Rust fungi and an excellent guide to the conservation status of those occurring in Wales; available for download from https://www.aber.ac.uk/waxcap/downloads.)